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SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

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May 19–20, 2000

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SYMPOSIA

Understanding the Urban Influence on Santa Monica Bay
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Research at Public Aquaria
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New and Rare Fish and Invertebrate Species in California during the 1997–98 El Nino
organized by Jim Allen (SCCWRP) (714) 894-2222

Conservation of California Lichens
organized by D. L. Magney (Consultant, California Lichen Society) (805) 646-6045

Los Angeles River Symposium
organized by Tina Hartney (Occidental College) thartney@oxy.edu

There will be additional sessions of Invited Papers and Posters and of papers by Junior Academy members.

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PLENARY ADDRESSES:

Plenary Sessions will occur each day at 11 a.m. Speakers will be;

Friday: **Wheeler North, "Kelp Beds of San Diego, Orange and Los Angeles Counties: Past, Present and Future Considerations."**

Saturday: **Joan Greenwood, "Friends of the Los Angeles River, River Watch; Addressing Watershed Issues in the New Millenium."**

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The Range, Habitat Requirements, and Abundance of the Orange-throated Whiptail, *Cnemidophorus hyperythrus beldingi*

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Abstract.—A survey was done over a 2½ year period on the Orange-throated Whiptail, *Cnemidophorus hyperythrus beldingi*, throughout its range in Southern California. The species has been presumed to be threatened by loss of habitat due to human activity. The study included determining the lizard's past and present distribution from museum and California Department of Fish and Game records, the literature, questionnaires, correspondence, and field surveys. Field surveys also were used to evaluate lizard habitat requirements and abundance. Detailed studies at the population level and laboratory and field studies on habitat requirements and behavior rounded out the study.

The range of the species can be defined as below 853m (2800 ft) elevation, with one record to 1058m (3,475 ft), from coastal and foothill Orange County, and from the Corona-Riverside-Colton areas of Riverside County southward through the Elsinore and Perris Basins, through all of the coastal and low elevation, San Diego County. Within its range, the Orange-throated Whiptail occurs primarily in open (50% cover) Coastal Sage Scrub vegetation, associated with Buckwheat (*Eriogonium fasciculatum*), low, open Chamise *Adenostoma fasciculatum*), White Sage and Black Sage (*Salvia apiana* and *S. mellifera*). The lizard also occurs in open chaparral, along the edge of open, dry, riparian areas, along trails, along dirt roads, and in areas of light off-road vehicle use.

This study has tripled the number of locations at which the lizard is known to occur, and has shown, by field work or correspondence, that the lizard still exists at 96% of all known localities. The whiptail occurs in large numbers locally (10–40 whiptails/hectare). A minimum estimate of 1 million Orange-throated Whiptails occur in the area of its range occupied by Coastal Sage Scrub and 10.1 million individuals within the area of the total range for this species in California. Even if these are over-estimates, they are over by a great many times the number needed in order to consider the species endangered. Estimates of habitat remaining for the species, range from 80–90% of values in 1900. The lizard does not meet any of the current criteria for listing as Rare, Threatened, Endangered, or Vulnerable. It is therefore not recommended for listing. Instead, Coastal Sage Scrub habitat should be protected wherever possible in open space and reserves.

The Orange-throated Whiptail Lizard, *Cnemidophorus hyperythrus beldingi*, a small striped teiid lizard, is listed in California as a "Species of Special Concern" (Natural Diversity Data Base 1994) and is a Federal Species of Concern (Federal Register 1996).

The Orange-throated Whiptail, hereafter referred to as whiptail or lizard, is the northern named subspecies of a series of subspecies that range from Orange and Riverside Counties, southward through San Diego County to the tip of Baja California and on some adjacent islands (Burt 1931; Murray 1955; Walker and Taylor 1968).

According to Bostic (1965, 1966 a,c) and McGurty (1980), the lizard occurs primarily in open coastal sage scrub vegetation. Termites constitute 57–95% of the whiptail's diet (Bostic 1966a). Additional foods consist of other soft-bodied arthropods such as spiders and insect larvae. The whiptail feeds by actively foraging in the leaf litter at the base of shrubs.

The whiptail has been found active every month of the year when soil temperature and air temperature are high (Bostic 1966b,c; Rowland 1992; Rowland and Brattstrom *in prep.*). It is a lizard with high thermal preference (36.8–41.6°C $\bar{x}$: 39.0°C; Brattstrom 1965), and hence is active on very warm, but not excessively hot days. The adults are especially active in the spring, with activity decreasing by mid-July. Young are hatched in August through October and are active through November, or if weather permits until December (Rowland and Brattstrom, unpublished data; Bostic 1966b). Adults are less active in the fall.

The lizard occurs in habitats that have been modified for agriculture and grazing, and in natural habitats that have been declining rapidly because of increasing human population impacts such as housing, highways and industrial development. With the presumed destruction of its natural habitat, the current distribution and population numbers of the whiptail were not known, hence the need for this study.

Materials and Methods

The Orange-throated Whiptail Lizard, *Cnemidophorus hyperythrus beldingi*, was studied in Orange, Riverside, San Diego, and San Bernardino Counties, California. Additional specific studies were done on three military bases: Miramar Naval Air Station, Fallbrook Naval Weapons Station, and Camp Pendleton (all in San Diego County); as well as a detailed mark and recapture study (Rowland 1992).

All laboratory, field activities, and research were done with a Memorandum of Understanding (MOU) from the California Department of Fish and Game (CDFG), the Guidelines for Use of Live Amphibians and Reptiles in Field Research of the ASIH, HL, and SSAR (as published in the Journal of Herpetology, supplement, 1987), the Public Health Service Policy on Humane Care and Use of Lab Animals (Rev. Ed., Sept. 1986), and the California State University, Fullerton, Animal Care, Committee Policies of the Office of Faculty Research.

To determine the past distribution of the whiptail, the distributional localities were obtained from museum records, the literature, and the California Natural Diversity Database (NDDB). Data were compiled and placed in R:Base 5000. A list of localities is available from the author. Locality data have been recorded on DeLorme maps, which consist of four 7.5 minute USGS Topo Maps. Locality data for the military bases have been placed into the U.S. Navy GIS Data Base only. All localities were also incorporated into OSUMAP software Geographic Information System (GIS). Records collected by Brian Mcgurty (to 1980) and Mark Jennings (to 1982) have been verified, sometimes corrected, and incorporated herein. Major United States and several local museum and university records were examined (see Brattstrom 1993, for list).

To determine the present distribution and abundance of this lizard, the historical distributional data and GIS maps of vegetation, soils, past fire history and current land use were prepared. Examination of these maps suggested that a few localities appeared to be in error, and that areas of apparent good habitat had no lizard locality records. In order to determine if the lizard actually occurred there and was missed by previous collectors or if this was poor habitat for the species, specific general areas (i.e., Moreno Valley, Perris Basin, Otay Mesa, Jamul) were selected for the 1989 summer and fall field surveys. Each area was explored by the lizard survey team (Dennis Strong and Brian Leatherman) for a week or two depending on the size of the area. The lizard survey team stopped randomly to survey for lizards wherever there was public access. If no lizards were found after a reasonable search (15–60 minutes), the team would move to another site. Sometimes this move involved a few hundred meters, sometimes kilometers.

In 1990, the survey team, in addition to working on the military bases, went to very specific locations and completed a transect, *whether lizards were found there or not.* Transects were also done in 1989 at localities where lizards were present. These specific locations were chosen in order to check habitat islands where records were missing, in an attempt to determine why whiptails were not present at some localities, to confirm whiptail presence at known historical or museum record localities, and to confirm or test the habitat quality index that was developed after the 1989 field season. During these surveys, two new techniques for collecting lizards were invented and developed (Strong et al 1993).

The present distribution and current status of the lizards was also determined by a survey questionnaire. The survey was sent to local professional and amateur herpetologists and herpetological clubs. In addition, the San Diego Herpetological Society and the Southwestern Herpetological Society reprinted this questionnaire in their respective newsletters. A total of 115 questionnaires were sent out and 50 questionnaires (or 43%) were returned. Of those returned, 33 surveys (or 29%) had information on whiptail distribution and abundance. With the use of questionnaires, correspondence, and actual field work, verification of whiptail presence, within the previous five years, was made at 103 (and possibly 113) of 116 of the previously known (museum and literature records) localities (Table 2).

Field transects were done in areas with and without lizards and in areas of different vegetation types and soil types. All transects were completed during thermally optimal times for the lizards (air temperature 15–42°C, soil temperature 25–55°C; Rowland 1992). All transects consisted of straight line transects that were 10m wide × 100m long. The length of the transect was oriented so as to be entirely within a single microhabitat. If a transect was one done only when a whiptail was seen, the survey was started, in so far as possible, at the location of the lizard sighting. If no lizards were sighted and a transect was to be done, it was usually located, in the center of a microhabitat and oriented so that the length of the transect was all in the same microhabitat. The exact locations and direction of surveys were recorded on large scale maps provided separately to CDFG (Thomas Guides) and the military (detailed maps they provided). With these maps, an interested investigator should be able to locate the survey line within 5m. In this sense, all transects are permanently recorded. At the start of a transect, the workers would complete a form with regard to location, elevation, weather, vegetation, topography and soil. The survey team would then walk the transect in one direction, counting lizards, and, on the return trip, count other on-site features such as ant mounds, rodent burrows, and logs. At the end of the transect, additional information on the presence of predators and past fire history was noted. In 1990, transects completed at military bases were done on very specific sites drawn *a priori* on vegetation maps provided by the bases. Transects were located in all vegetation types on the base and each vegetation type had several transects. Transects were further located so as to sample the same vegetation type in different parts of the base. While a large part of each base consisted of open space and even reserves, some parts of each base could not be surveyed due to military activity or installations. Lizard surveys were done on the bases whether lizards were present or not. Lizard transects on the bases were repeated about a month or two following the original survey. Detailed data for the bases are presented in separate reports to the military and CDFG.

Transects were intended to assess habitat requirements quantitatively and not necessarily to characterize a specific location. Transect data and habitat characteristics were quantified in a series of graphs and tables. These data were then used to construct a Habitat Quality Index (HQI) for the Orange-throated Whiptail. A scale of poor to good habitat was developed for each of the variables tallied. For example, whichever habitat characteristic had the most lizards on it (i.e. the tallest bar on the graph; Figs. 3,4) was ranked high. A habitat with no or few lizards ranked low. Those with intermediate numbers of lizards ranked medium. The characteristic and its conditions are presented as the HQI. Using 12 characters, and the ranking of each character (high, medium, low), each character can be scored by any surveyor so that a number can be given to each habitat. Scores of 0–12 result in a low designation, 13–24 are medium, and 25–36 rank as high. A potential habitat can thus be graded as poor to good for an Orange-throated Whiptail without having to see a lizard present. The HQI is simple enough so that it can be completed by most field-trained biologists. It allows the habitat to be quantified in times and seasons when lizards are not active. It must be used, like all other evaluation forms, with caution. Field soil size was determined based on the standard U.S. Forest Service and U.S. Soil Conservation Corps methods; coarse soil (large grain size, does not roll between fingers), sand (intermediate size, rolls between fingers), or fine soil (small grain size, does not roll between fingers). Laboratory experiments were conducted at California State University, Fullerton, between June 28 and August 24, 1989. Three aquarium tanks measuring 60cm × 53cm were each divided into quadrants by cardboard. Four different substrates were put into each one of the quadrants. The gravels and soils were sifted through various sized screens to achieve a basically uniform size in each quadrant. The grains were counted and sized individually under a dissecting scope. The photoperiod for these experiments was provided by white IR and vitalite lamps on between 0700 and 2000. The ambient temperature was kept between 15°C and 21°C.

GIS Analysis

To further analyze the habitat and distributional information, Orange-throated Whiptail locality data were entered into a Geographic Information System (GIS) using OSUMAP software. Other data put into the program included: elevation, vegetation, rainfall, basic geology, fire history, known open spaces (including parks, reserves, and forests), and urban areas. Locality data for lizards on the military bases was put directly into their GIS system by Tierra Data, Inc. where other ecological data was already stored. The combined information was examined for the base reports.

Abundance

In addition to range and habitat requirements, it is also important to know how many lizards occur in a given area, habitat, or its entire range. Lizard survey transects were 10 × 100 meters. Lizard abundance per transect, per hectare, or the number of lizards seen per person-hour was calculated. To test whether transects were counting lizards effectively, the survey team completed a typical lizard transect on the permanent study plot of Scott Rowland (1992) located on the Motte-Rimrock Reserve on September 25, 1990. Study plot personnel did not know when survey teams would check the site and the survey team did not know how many lizards had been marked on the site, thus this was a double blind test for the field transects. Two passes (each 10 × 100m) were made on the 100m × 100m study plot. The average number of lizards seen on the two surveys was multiplied by 10 to give the number of lizards per hectare. That number should be close to the known number of marked lizards (from mark-recapture studies) on the site.

While habitat destruction decreases the amount of habitat available to these lizards daily, some measure of habitat availability is needed to estimate population numbers, therefore the total area of Coastal Sage Scrub in Southern California was determined from the literature (Atwood 1992; Minnich 1983) and then the amount of that vegetation within the actual range of the whiptail was calculated from GIS data. This area was multiplied by the lowest (conservative) value of the field-determined lizard densities per hectare. This provides an estimate of the minimum number of these lizards in Southern California. This is a minimal number since, while the lizard occurs primarily in Coastal Sage Scrub, it also occurs in a variety of other habitats, including some disturbed habitats. It assumes that all such habitat is equally suitable for the lizard. Field data clearly indicate that this is not true. Some Coastal age Scrub and some transects had no lizards, but other transects had many lizards and extensive areas of other habitats that had whiptails are not included in calculations. Hence, transects and areas with no lizards, hopefully, will average out in these estimates. The function of this analysis was to determine at least some order of magnitude of the number of whiptails in California. For the same reasons, estimates were also made of the minimal numbers of lizards throughout its range, even though the whiptail is not equally distributed. It was not the function of this analysis to determine an absolute number of animals, but only a minimal estimate. This method of determining population estimates is similar to that used with birds and mammals, including rhinos, elephants, and tigers (Atwood 1992) but has seldom been used with lizards.

In order to study the characteristics of whiptail population structure, a 1 hectare study site was selected at the Motte-Rimrock Reserve of the University of California, in Perris, Riverside County, California; and activity, population structure, home range and reproductive activity were studied by Scott Rowland (1992). These studies and additional information from the main study are being published elsewhere (Rowland and Brattstrom *in prep.*)

Results

Distribution

Figures 1 and 5 show the range and distribution of the Orange-throated Whiptail, *Cnemidophorus hyperythrus beldingi,* in Southern California. The range of the species continues southward to the tip of Baja California, Mexico and some adjacent islands. Lists of all known locality records for the species in Southern California and detailed dot-locality maps are presented in Brattstrom (1993) and are available from the author. The localities have been entered also into Bureau of Land Management (BLM) Data Bases for Southern California, and into several other County, Environmental Companies', and U.S. Navy and Marine Data Bases. The localities have not yet been entered into the CDF&G National Diversity Data Base (NDDB).

Figure 2 presents the elevation records for the locality records. As can be seen, 99% of all locality records are below 3000ft (913m). In fact all records, except one, are below 2800 feet (853m). The lone exception is a record at 3475 ft (1058m) about 11km NE of Aguanga, Riverside County. This is a very open, dry area of Riversidian Coastal Sage Scrub. Many low elevation species, including Stephen's Kangaroo Rat, *Dipodomys stephensi,* occur at higher elevations in this area. A CDF&G NDDB record (#105) of 3400 ft (1036m) at "Cahuila Road, North of Aguanga" is in error, the elevation is 2400 ft (731m) according to the collector).

There are 116 historical records for this species based on museum records (Table 1, 2). Whiptails were first collected in San Diego County in 1891, in Riverside County in 1893, and not until 1946 in Orange County. Field work, questionnaires, and correspondence tripled the number of known localities for the species to 343 (Table 2). Since the majority (66%) of these localities come from this study (including 26% from the 1989–91 field surveys), it indicates that the whiptail has been seen at these additional 227 sites sometime since 1985. Field work in this study, data from questionnaires, and correspondence (including asking colleagues to please go out to a given locality and check for the lizard's presence) have confirmed (=verified) the whiptail's presence in 1985–1993 at 103 of the 116 literature, historical, and museum localities. Thus the Whiptail is present at 96% of all known localities.

The word locality or record refers to a known location where specimens of the species have been collected or seen. In some detailed environmental studies, lizards are reported at localities only .1 or .5 miles apart. In other cases, it is impossible to know, without detailed notes, where, for example, in the locality "San Diego", these lizards may have been actually collected. Localities given as city suburbs or parks within a city, for example San Diego, are placed at those locations on the map and are considered as different localities. Collections made in different years by different collectors from a location as vague and as large an area as the city of San Diego are treated as separate localities for purposes of calculation, but are plotted as a single dot. The words exist or extant are used if a population of whiptails still occurs at a location and extinct if a former or known population no longer occurs at a specific location. Many conservation biologists like to use the word extirpated rather than extinction for local populations. By definition, extirpation requires that the absence is due to *human* causes. The cause

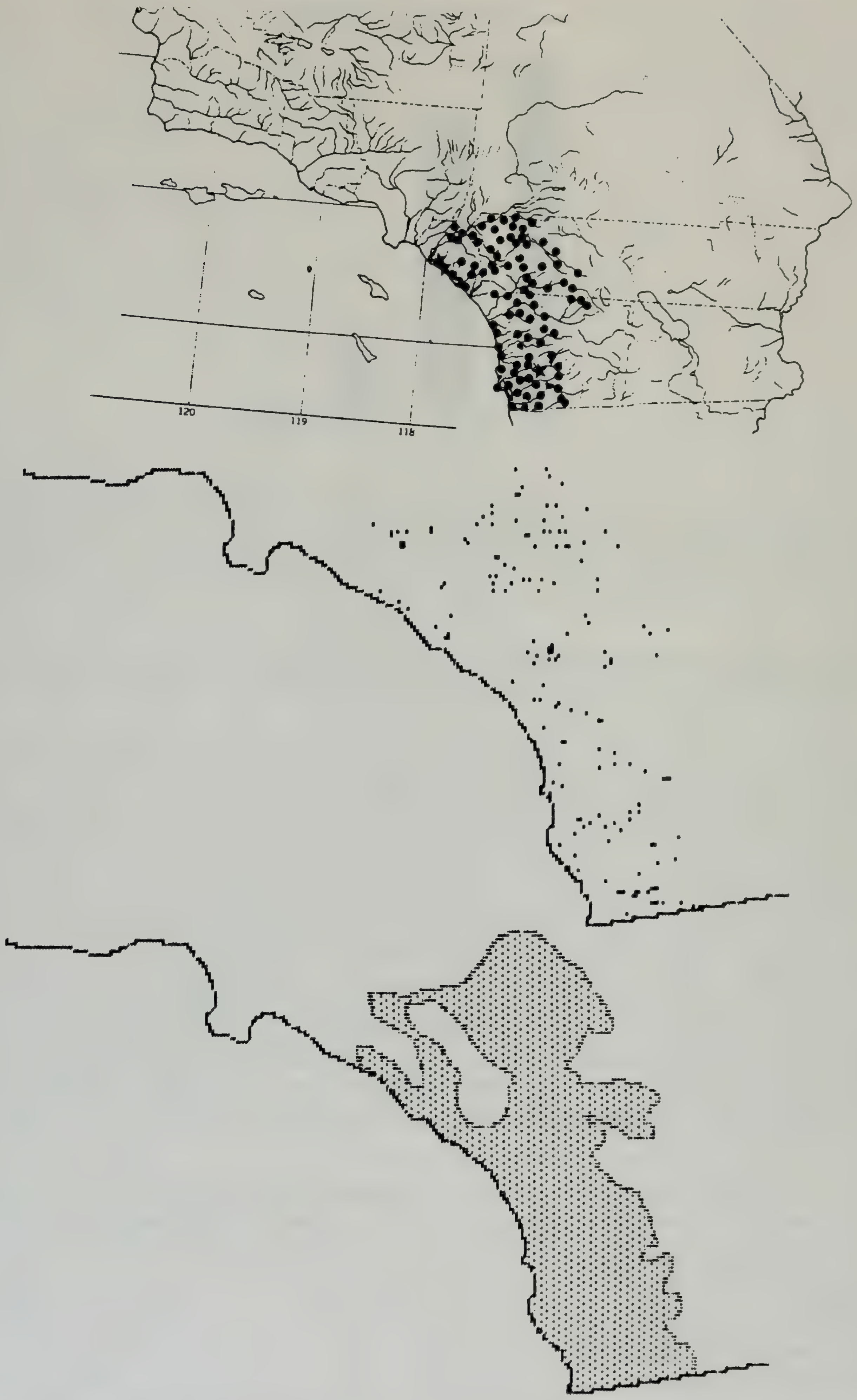


Fig. 1. Three maps of Southern California showing the range and distribution of the Orange-throated Whiptail, *Cnemidophorus hyperythrus beldingi.* Upper: verified extant (dots) and extinct (stars). Middle: GIS plot of all locality records. Lower: GIS produced map of range. Due to space and scale not all localities could be plotted.

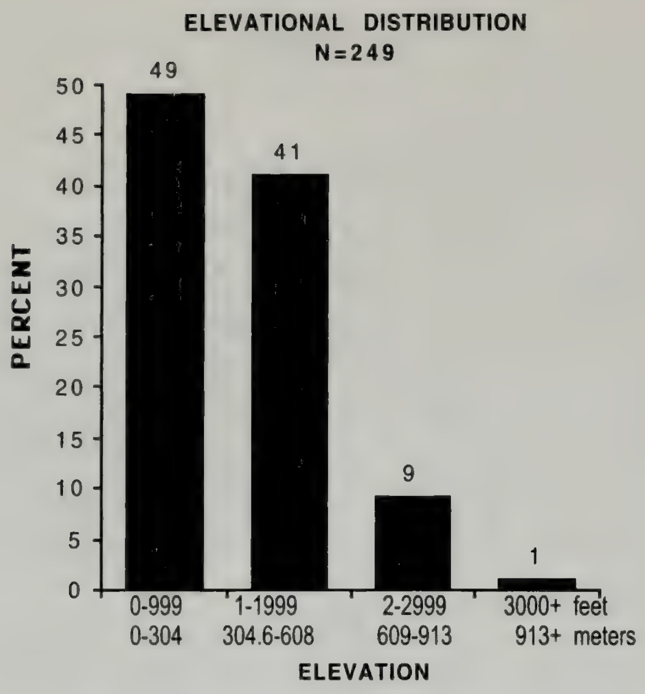


Fig. 2. Graph showing the distribution of elevation records of the Orange-throated Whiptail, *Cnemidophorus hyperythrus beldingi*, in Southern California. Numbers at top of bars are percent of total localities. All but one record (at 3475 feet; 1058m) are below 2800 feet (853m), and 90% of all records are below 2000 feet (608m).

for the animal's absence is clearly due to human events (as in the paving over of the San Diego State University Campus locality) but in other cases the cause is not known; therefore I use the word extinct. On the other hand, just because an area is now urbanized, the assumption can not be made that the lizards must have occurred there before. The historical data argue otherwise. There are, for example, no historical (literature or museum) records for this whiptail in west, central, or north Orange County, All Orange County records are from Corona del Mar and the Laguna (=San Joaquin) Hills southward, and from Santa Ana Canyon and south. Whether their absence from the north, central, and western flat area of Orange County is due to disturbance by grazing and agriculture for the 400 years (Cleland 1941, 1952) prior to the first museum records (1946) or whether this area was not covered by suitable habitat is unknown. Extinction and rapid reinvasion of areas and new invasions of new areas appears to be one of the results of the r-selected reproductive mode and dispersal of this whiptail (Bostic 1966c: Rowland 1992). This dispersal results in whiptails being present in some locations

Table 1. *Cnemidophorus hyperythrus* locality records listed by county.

	Riverside	San Diego	Orange	San Bernardino	Total
Literature and Museum					
(1891–1985)	60	44	10	2	116
Correspondence & Questionnaires					
(1985–1991)	69	83	15	0	167
Surveys (This study)					
1989	16	10	0	0	26
1990	11	9	3	0	23
Bases	na	11	na	na	11
Total	156	157	28	2	343

Table 2. Comparison of historical and recent (post 1985) locality records for *Cnemidophorus hyperythrus*.

	Number
Literature and Museum Records	116
Species extinct at:	3*
Species probably extinct at:	10*
Species probably still existing at:	10
Species still existing at (verified):	103
Additional Recent Locations based on Correspondence & Questionnaires	167
Additional Recent Locations based on field surveys:	
1989:	26
1990:	23
Bases:	11
Total:	60
Total known localities:	343
Total known localities with verified, existing populations	330

* Extinct and probably extinct at 11% of the originally known historical museum locations. Extinct locations: San Diego State University Campus in San Diego County; 1 mile southeast of Corona del Mar and Corona del Mar Bluff in Orange County. These Orange County locations may not really be extinct at the population level, as there are recent verified records (June 1991) for Crystal Cove and Pelican Hill, which are within three miles of Corona del Mar.

** With the addition of the populations added from this study, the species is extinct at only 1% of a total possible 343 locations, and extinct or probably extinct at 3.8% of all possible localities.

where they were not present a year or two before. In contrast, an area with lizards in one month or year may be devoid of them in a later month or year, only to be repopulated again shortly. Often the lizards may be absent from a specific area of land where they occurred last year or five years ago, only to be 200 meters away. These local changes may be due to local population dynamics and/or subtle habitat changes that take place over the years of data records. In any event, even historical localities have been checked and given the arbitrarily selected error of 5 miles (equivalent to the space covered by one dot in Figure 1) the whiptails still exist (i.e. verified presence since 1985) at 103 of the 116 or 89% of all known historical localities and 96% of all known localities (Table 1, 2). The species is extinct at three localities. This is less than 1% of *all* known localities. The extinct localities are: San Diego State University Campus in San Diego County; 1 mile southeast of Corona del Mar, and Corona del Mar Bluff in Orange County. These Orange County populations may not be really extinct (and thus don't meet the definition of extinction) as there are recent, verified records (June, 1991) for Crystal Cove and Pelican Hill, which are within three miles of Corona del Mar. The species may be extinct (lizard presence possible, but not verified) at 10 additional locations, thus the total extinct or probable extinct number of localities is 13 or 3.8% of all known locations (i.e. the species is known to exist, 1985–91, at 96% of all known 343 localities). The total range occupied by whiptails is shown in Figures 1 and 5. While urban and suburban development occupy much of this area (Fig. 5), and since the lizard still exists at 96% of all known localities, the lizard appears to be co-existing with some, but not all, human habitat disturbance. Analysis of the GIS data suggest that 40% of the lizard's original habitat is occupied by human activities or is otherwise disturbed. Yet, based on field work, an examination of GIS and range data, and due to the diverse topography of Southern California, the lizard still exists in most of its original range. For example, lizards are still present (verified by field observations) on U.S. Navy property at the tip of Point Loma, San Diego County where they were collected in 1893! The species still occurs in coastal sage scrub canyons within Balboa Park, a park completely surrounded by the city of San Diego. The lizard was also found, to be present in high numbers along such human disturbances as railroad tracks, freeways, xerophytically planted yards, and in open riparian areas.

In summary, in California, the Orange-throated Whiptail occurs from sea level to 853m, (except north of Aguanga where it occurs at higher elevations), in Orange, Riverside, and San Diego Counties essentially south of California State Highway 91 and Interstate Highway 10. The species occurs north of Hwy 91 only in east Norco and within the city of Riverside. The species occurs north of State Highway 60, only in the Riverside City, Box Canyon, Pigeon Pass Valley, Reche Canyon area. Two localities ("Reche Canyon near Colton" and "2 miles up Reche Canyon") are old records and are so vague that it is not clear whether the localities should be located in Riverside or San Bernardino County. They are listed for San Bernardino County in Table 1. The species exists today in Reche Canyon, but in Riverside County. Perhaps these historical records are for Riverside County as well.

Several erroneous locality records for the whiptail were discovered in the literature, museum records, and the CDFG NDDB. Most of these records are based on errors of identification of specimens, clerical errors by collectors, errors by museum catalog personnel, or simple typographic errors. Museum curators have been advised of these errors. The following locations are *NOT VALID LOCALITY RECORDS*: San Diego County: 3 mi. S Buckman's (clerical error); 18 miles E of Julian (clerical error for W of Julian, but that location has the wrong habitat and elevation); San Bernardino County: Cajon Wash, 2.5 air miles SE of Devore (error of identification; LaPre, personal communication; the specimen was a *Cnemidophorus tigris*); Riverside County: End of Whitewater Canyon by trout farm, and Jenson Canyon, San Gorgonio Pass (clerical error by collector; both localities have creosote bush habitat and both sites were examined several times during this study and only *C. tigris* was present).

Habitat Requirements

Field surveys were designed to obtain habitat as well as distributional data Raw data for all lizard surveys are presented in Brattstrom (1993) and are available from CDFG or the author. A total of 362 survey-transects were completed: 274 were on military bases, 88 of these were not. Of the 362 surveys, 65 of them had lizards on the transect, 49 (13.5%) had whiptails.

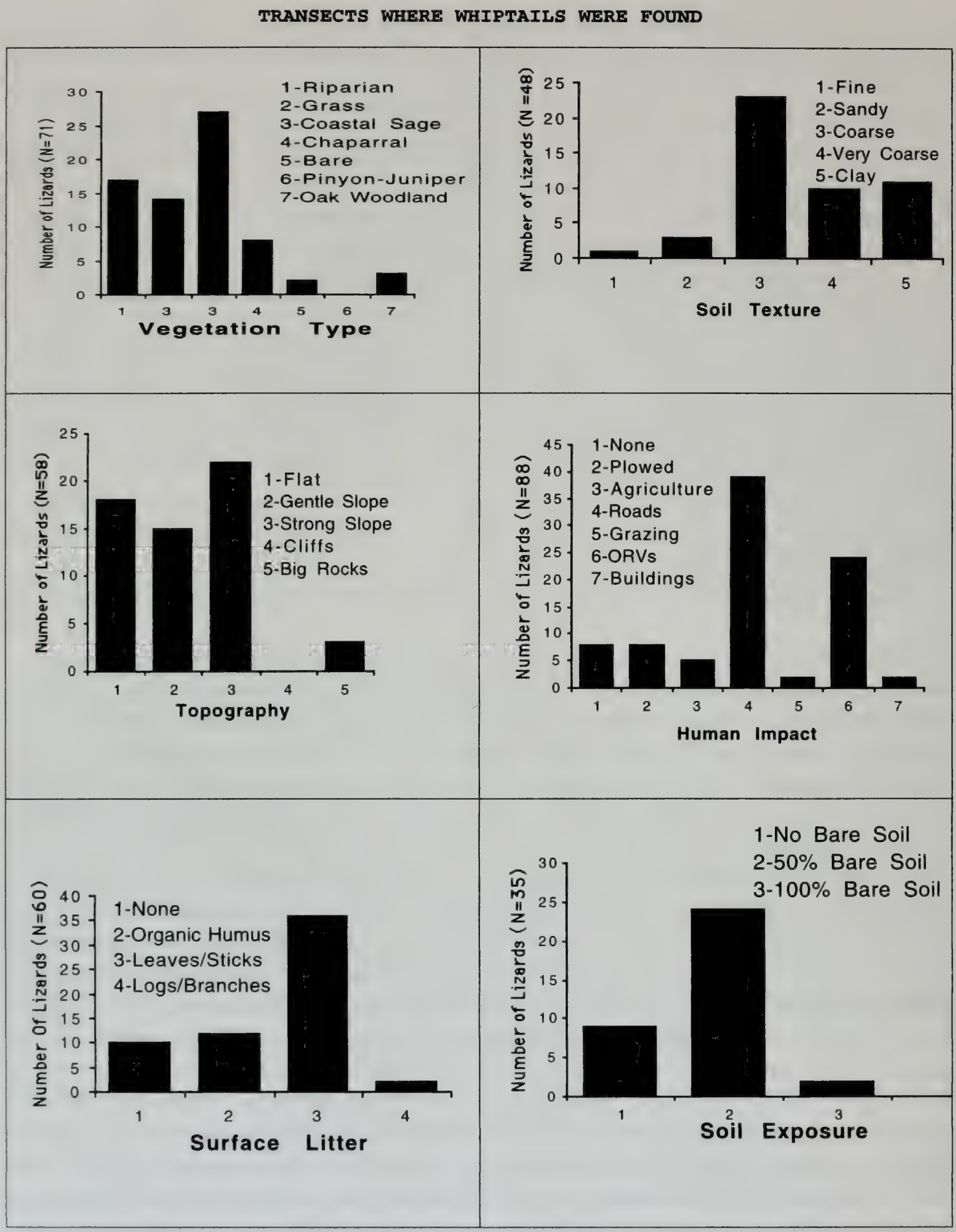
On all surveys, dominant plants were listed in order of apparent numerical dominance by visual estimate. Notes were also taken on whether grasses, mustard, and wild oats (see Table 3 for scientific names) were present. The latter two suggest past human disturbance. Table 3 shows that Orange-throated Whiptails are found predominantly in areas with Buckwheat (70% of surveys), Chamise (65%) and White Sage (35%). Black Sage (26%), and California Sagebrush (13%), Mule Fat (9%) and Laurel Sumac (13%) were present on some surveys. Buckwheat, White Sage, Black Sage, and California Sagebrush are the charac-

Table 3. Rank order of species of perennial and annual plants on 32 surveys with *Cnemidophorus hyperythrus* based on occurrence and dominance. The rank order describes habitat for Orange-throated Whiptails and is a useful predictor of its occurrence.

PERENNIALS	% of Surveys
1. California Buckwheat, *Eriogonum fasciculatum*	70
2. Chamise, *Adenostoma fasciculatum*	65
3. White Sage, *Salvia apiana*	35
4. Black Sage, *Salvia mellifera*	26
5. California Sagebrush, *Artemisia californica*	13
6. Laurel Sumac, *Malosma laurina*	13
7. Mule Fat, *Baccharis salicifolia*	9
8. Prickly-pear Cactus, *Opuntia sp.*	6
9. Deer Weed, *Lotus scoparius*	3
10. Scrub Oak, *Quercus dumosa*	3
11. Mexican Elderberry, *Sambucus mexicana*	3
12. Lemonade Berry, *Rhus integrifolia*	3
ANNUALS	
1. Grasses	59
2. Mustard, *Brassica sp.*	59
3. Wild Oats, *Avena fatua*	28

teristic species of Coastal Sage Scrub vegetation in the range of the whiptail. Other members of the Coastal Sage Scrub and Chaparral plant communities were present on less than 6% of the plots. Chamise, *Adenostoma fasciculatum*, is normally considered to be a member of the chaparral plant community, but in inland Riverside and San Diego Counties and coastal Orange County and San Diego Counties, Chamise also occurs within the typical Coastal Sage Scrub Vegetation Type (Buckwheat, Black and White Sage, California Sagebrush). In these areas Chamise is usually low (less than 1m high) and wide spread, in contrast to its tall (to 4m), dense (*ie* 100% cover) occurrence in chaparral. The presence of Chamise in Coastal Sage Scrub vegetation is not inconsistent with the low, open nature of that vegetation type. Orange-throated Whiptails thus prefer Coastal Sage Scrub vegetation with Buckwheat, Chamise, White and Black Sage. Mustard and grasses were present in 59% of Orange-throated Whiptail surveys. The weedy Wild Oats, *Avena fatua*, was present in only 28% of surveys. Vegetation alone is not always a good predictor of whiptail presence as 25% of transects in Coastal Sage Scrub did not have whiptails (Fig. 4) and whiptails did occur in other habitats. Other habitat characteristics such as cover, soil, and slope, also important for whiptails may not have been suitable at those sites.

Figure 3 presents the data for habitat variables on transects where whiptails were present. The same data expressed as "percent of lizards" and "percent of transects with lizards" are presented in Brattstrom (1993). They do not differ in any significant way from Figure 3. Figure 4 presents data for transects where *no* whiptails were found. Some of these graphs are the opposite of graphs for the same variable where whiptails *are* found indicating that certain characters are especially important. Yet other graphs (Fig. 4) show that similar habitats may not have whiptails. This is probably due to the fact that not all variables are in sync or that populations of whiptails were low at that site. For example, whiptails are



TRANSECTS WHERE WHIPTAILS WERE FOUND

Fig. 3. Habitat characteristics of Orange-throated Whiptails based on transects where whiptails were found. Topography: Flat: 0–15; Gentle: 15–45; Strong: greater than 45 slope. Because topography on a single transect may vary, some transects had two or more categories. Soil categories are USDA Soil Conservation Service categories and are defined in the text. Roads: any type from paved to dirt. ORV: any indication of ORV activity.

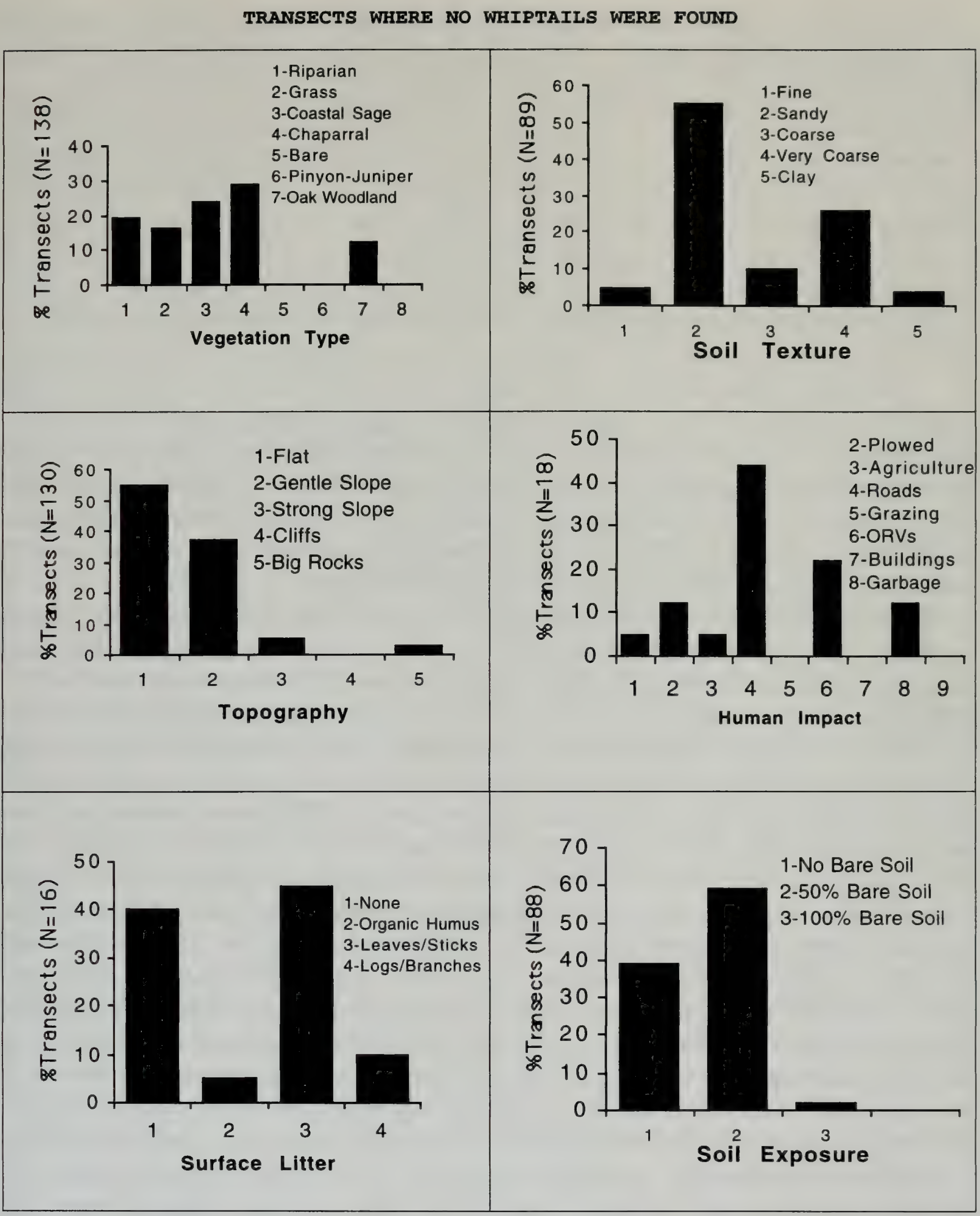

TRANSECTS WHERE NO WHIPTAILS WERE FOUND

Fig. 4. Habitat characteristics of transects made where *no* Orange-throated Whiptails were found. Categories are the same as in Figure 3.

most often found in Coastal Sage Scrub vegetation, but not all Coastal Sage Scrub habitat had whiptails (Fig. 4). Note further that whiptails are found where there is leaf litter (Fig. 3), but some sites with leaf litter (Fig. 4) did not have whiptails. Perhaps, in spite of the presence of leaf litter some other characteristic was not right for the whiptail.

To summarize the habitat data, Figure 3 indicates that Orange-throated Whiptails are found primarily in Coastal Sage Scrub vegetation. They are also found

Table 4. Soil size choice of *Cnemidophorus hyperythrus* in laboratory experiments where four choices of soil size were available. (N = 3 and tally times = 5, so total choices = 15.) One lizard had not made a choice during one tally, so the numbers are given as a percent of 14 choices.

Soil size names	Size of soil*	Percent of lizards choosing
Fine	0.1–0.5 (0.39)	0
Medium	0.5–2.6 (1.8)	100
Coarse	3.0–6.4 (4.6)	0
Very Coarse	9.0–15.2 (11.6)	0

* Soil sizes are given as a range and a mean size in mm. based on microscopic examination.

in grassy areas and in broad open disturbed riparian areas. Whiptails also occur in chaparral, but the chaparral must be open. Whiptails occur in flat, gentle (15°), and even strong slope (45°) areas, but not on cliffs (Table 5). Whiptails were most often found in areas with 50% cover and 50% bare soil. The absence of vegetation (100% bare soil) implies the absence of food, and the few lizards present on such surveys may have been just passing through these areas.

Whiptails are found primarily on coarse soil (see definition above), and almost never on fine soil, or sand. However, in laboratory experiments (Table 4), these lizards selected medium soil 100% of the time in a four soil-size choice experiment. Whiptails dig their own burrows and seldom utilize rodent burrows except for extreme emergencies (Rowland 1992; Bostic 1965, 1966 b,c). A coarse soil must be important in holding the lizard-sized burrows open and medium sized soil may be easier for this small lizard to escape in. While most transects did not have roads or paths on them, Figure 3 shows that when present, whiptails are found most often on transects which have a dirt road or a few off-road vehicle paths. This is probably due to the fact that both off-road vehicle activity and dirt road construction break up hard surface soil, make a slope of loose coarse soil, or make a side berm of coarse materials. These coarse soil slopes and berms are where whiptails dig their burrows and lay their eggs (Bostic 1966c). Presumably, for this same reason, whiptails are also commonly found along the edge of hiking and equestrian trails and along fences. In fact, even though transects were done through dense chaparral, the only incursion of whiptails into chaparral vegetation is along roads, trails, and fences. Historically this disturbance and trail making presumably was done by erosion and large, now extinct, mammals. Note that whiptails are seldom found in plowed fields or fields with agricultural crops (Fig. 3). They are seldom found about buildings, though two correspondents who lived in open Coastal Sage Scrub vegetation reported whiptails in yards, even coming into xerophytically planted patios to feed. Figure 3 clearly indicates that whiptails do better with some light human disturbance such as roads and trails (see also Walker and Cordes 1990). Interestingly, whiptails are often found (personal observation) where people have dumped garden and other debris.

Whiptails eat primarily termites (Bostic 1966a). It is therefore not surprising to find that more whiptails occur in habitats with more leaves and small sticks (Fig. 3). They are not found in areas with large logs or even lots of logs. This is consistent with the rapid leaf litter foraging method of whiptails. Termites within large logs would be unavailable to the lizards and an abundance of logs may interfere with their need for open running room. Their presence about human debris may be due to the nature of that debris in attracting termites. Whiptails do not occur in areas where the number of harvester ant mounds is high which suggests that in open areas whiptails are not common in exactly the same microhabitat as Coast Horned Lizards, *Phrynosoma coronatum* (which feed on the ants) (Brattstrom 1997; Hager and Brattstrom 1997). It may also be that whiptails are affected by the bites of the ants and choose to avoid them. Whiptails were not found in areas with lots of ground squirrel, gopher, and other rodent burrows. This may be due to the fact that these lizards make their own burrows, seldom use rodent burrows for escape, or that the rodents disturb the area or leaf litter too much. In addition, predators that dig rodents out of burrows such as skunks and fox, would also find and eat whiptails if they were in rodent burrows.

One of the original working hypotheses was that large numbers of whiptails would occur in areas following fires. The idea was that after a fire there would be a lot of dead wood which would attract termites, the main food of whiptails. Orange-throated Whiptails in fact were usually found in areas (17/22 transects or 77%) that have *not* been burned recently (within the last 5 years). This supports observations that these lizards feed on termites in leaf litter under bushes. Fires would destroy that leaf litter and termites within logs would not be available to this small lizard.

The Orange-throated Whiptail is a high thermophilic basking lizard and like teiids in general has a higher body temperature (36.8–41.6°C, $\bar{x}$:39.0°C) than sympatric phrynosomatid lizards (Brattstrom 1965). Transect data and Rowland (1992) showed that whiptails are not found out of retreats until the soil temperature is greater than 21°C for juveniles and 24°C for adults and air temperature is greater than 12°C for juveniles and 21°C for adults. They are out on very hot days (30–50°C), but are not found out when soil or air temperature exceeds 55°C (Rowland 1992; Rowland and Brattstrom in prep.). In addition, high environmental temperatures associated with the low humidities in their habitat cause rapid water loss due to evaporative cooling from mouth and lungs during respiration (which is very high at these temperatures and for this small lizard). As a result, like many such thermophilic lizards, the whiptail is inactive on some otherwise ideal days or some parts of the day, presumably, in order to conserve water.

Figure 4 shows some of the characteristics of transects where *no* Orange-throated Whiptails were found. Most of these graphs are the reciprocal or reverse of Figure 3 as this or some associated characteristic was not suitable for whiptails. In some cases no lizards were found on transects with some of the same characteristics as areas with lizards. Whiptails may have been on the transect but not seen. It is more likely, that while the area met one of these variables (ex. road) it did not meet another (50% cover). In other cases, sites looked just like similar sites with lizards. The lizard could have become extinct on that site, might never occurred on that site, or were not there because of other reasons (lack of termites) or because of some variable that we did not measure.

In summary, Orange-throated Whiptails are found primarily on Coastal Sage Scrub vegetation with Buckwheat, Chamise, White Sage and occasionally Black Sage, with 50% of the land bare (=50% cover), in flat to sloping topography, in areas with leaves and small sticks under bushes, no evidence of fire, few or no ant mounds or rodent burrows, in coarse soil, with some loose dirt, as along dirt roads and trails, and below 853m (max. 1058m) elevation in Coastal Orange, Riverside, San Diego Counties of California and southward to the tip of Baja California.

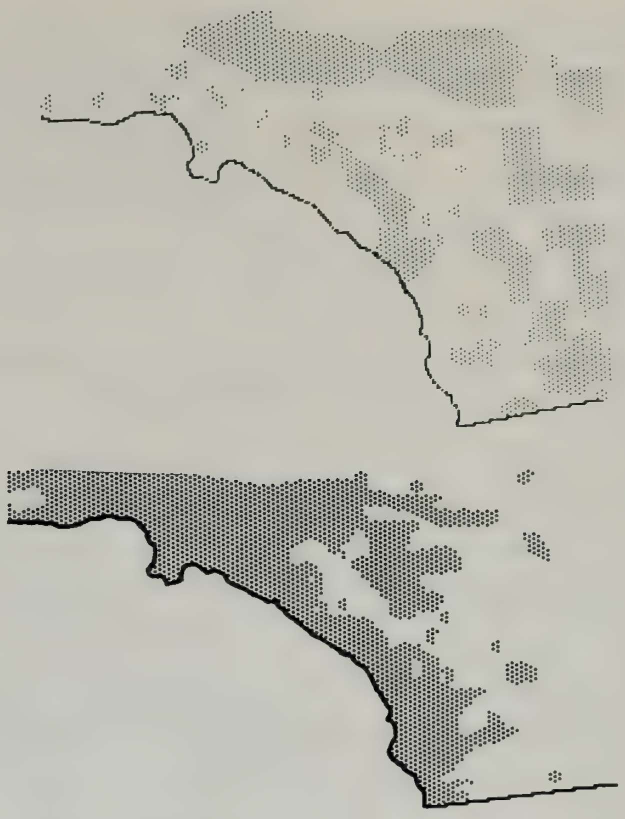
GIS Analysis

To further analyze the habitat and distributional information, the distribution of whiptails (locations from dots on maps Figure 1, and Brattstrom 1993) of the whiptail was entered into a OSUMAP-GIS program. Other data put into the program included: elevation, vegetation, rainfall, basic geology, fires, known open spaces (including parks, reserves, forests), and urban areas. Some of the resultant maps are presented in Figure 5. For calculation of areas of land use, the maps have been overlaid on a light table, and the area estimated visually using a graph paper overlay. There is thus an error in these area estimates which is a function of the size and scale of the map and the use of any GIS program at the scale of all of Southern California. The GIS maps support the basic observations made from field surveys: 1) Whiptails are found in the coastal and inland physiographic zone; 2) they are found primarily in Coastal Sage Scrub vegetation; 3) they are not found in areas of fire; 4) their range includes urban and suburban land; 5) about 40% of the known localities occur in public lands, parks and reserves. There are many advantages to GIS analysis, but many of these advantages disappeared when covering a large area, and where habitat variables have small and patchy distributions (such as vegetation or soil type on different slopes of a small hill).

Habitat Quality Index

A Habitat Quality Index (HQI) was made (Table 5) for the Orange-throated Whiptail by utilizing characters and their conditions presented in the graphs and tables just discussed. A scale of poor to good habitat was developed based on the quality of that habitat for each of the variables tallied. For example, for a variable such as vegetation or soil, that habitat characteristic which had the most lizards on it (i.e. the tallest bar on the graph or highest number on a table) was ranked high. A habitat with no or few lizards ranked low. Those with intermediate conditions were ranked medium. Using these 12 characters (numbers 2 and 3, Cover and Percent Bare Soil, are reciprocals of each other), any given habitat can be quantitatively placed into a low, medium, or high (C, B, or A grade) category. A habitat thus can be quantified as being poor to good for a whiptail without even having to see a lizard present. The HQI is simple enough to be completed by most field trained biologists. It allows the habitat to be quantified at times and seasons when lizards are not active. It must be used, like all such evaluation forms, with caution. It is a method for determining and quantifying potential habitat, not lizard presence. Quantitative data (Fig. 3) allow the prediction that those habitats with high rating probably do have whiptails present. The transect, characters tallied, and HQI has been adapted, slightly modified, for habitat characterization under California's Coastal Sage Scrub Natural Community Conservation Planning process (CSS/NCCP) guidelines.

Whiptails occasionally occur in peculiar habitats, such as in the exotic Ice Plant, *Carpobrotus edulis*, at the upper edges of beaches. Whiptails occasionally forage in open riparian areas, such as those with Sycamore and thick brush.



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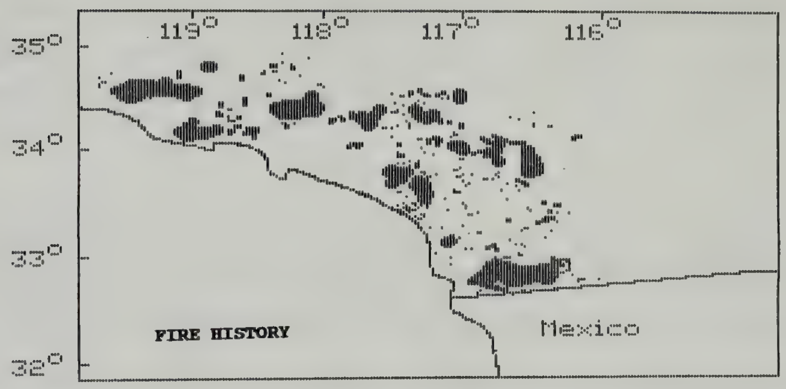

Fig. 5. GIS analysis of some habitat information on Orange-throated Whiptails. Maps are of Southern California and cover about the same area as Figure 1. The bottom of each map is the U.S.-Mexico border and the peninsula in the upper left part of the maps in Palos Verdes of southwestern Los Angeles County. Note that the fire history map is at a different scale due to data source. Maps of Parks, reserves, National Forests (Upper), and urban and Suburban land use(middle) are original data. Names and acres of parks are from Brattstrom (1993). The fire map comes mostly from Minnich (1983), with more recent fires added. There is apparent overlap between the range maps (Fig. 1) and the urban and suburban land use map as whiptails occur in some of these areas and because the GIS process at this scale cannot discriminate between, for example, a housing development on a hill from the Coastal Sage Scrub covered slopes which mat be occupied by whiptails.

Abundance

Lizard survey/transects were 10 × 100 meters. On transects with lizards, from 1 to 4 lizards occurred per transect (18 transects had one lizard, 8 had two, 4 had three, and 5 had four lizards) with a mean (64 lizards on 35 transects) or 1.8 lizards in a 10 × 100m area multiplied by 10 gives 10–40 lizards/hectare. The number of lizards seen ranged from 3 to 48 lizards per man hour.

To test whether the lizard surveys were effectively counting (i.e. seeing) lizards on transects, the lizard survey team did a typical lizard transect on Scott Row-

Table 5. Habitat Quality Index for *Cnemidophorus hyperythrus.*

Character	Low = C = 1	Medium = B = 2	High = A = 3
1. Vegetation	Bare	Grass, chaparral, riparian edge	Coastal Sage scrub
2. Cover	0%	100%	50%
3. Percent Bare Soil	100%	0%	50%
4. Soil Texture	Fine/sandy	Clay	Coarse–medium
5. Surface litter	Bare or logs & branches	Organic humus	Leaves and sticks under bushes
6. Slope	Cliffs	Flat* 0–15°	Gentle to strong* 15–45°
7. Annual Plants	*Erodium* only, agriculture	Wild Oats only	Grasses, including wild oats: mustard
8. Perennial Plants[1]	Bare or thick chaparral	Mule-fat, Laurel Sumac. Calif. Sagebrush	Buckwheat**, Chamise, White Sage, Black Sage
9. Fire History	Recent fire	Fire within last 5 years	No evidence of fire
10. Number of gopher and grd. squirrel burrows	High 75/100m	Medium 25–75/100m	Low 0–25/100m
11. Human Impact	Plowing, grading, agriculture, buildings	ORV activity	Dirt roads especially with berm or raised shoulder
12. Other Lizards	*C. tigris*	*Sceloporus*	*Uta*
13. Predators Present	None	Scrub Jay, Northern Mockingbird, Shrike	Whipsnake/Racers*** Road runner Kestrel
Temperature Constraints****			
Air Temp.	17–29° C	30–35° C	36–42° C
Soil Temp.	25–34° C	35–45° C	45–55° C

* rocks O.K.
** listed in order of importance
*** *Masticophus* and *Coluber*
**** These are the bad, good, and better times to assess the habitats if actually looking for or counting lizards.
[1] In beach habitats, ice plant and other strand vegetation *may* be good indicators.

land's permanent 100 × 100m study plot on the Motte-Rimrock Reserve on September 25, 1990. In each of two passes (each 10 × 100m) on the study plot, 3 OTWs were observed (for a total of 6 lizards). Based on 3 lizards per 10 × 100m transect, multiplied by 10 to equal the size of the 100 × 100m study plot give numbers that generates an estimate of a total of 30 lizards/hectare. By this date Scott Rowland had 24 lizards marked and calculated (Rowland 1992) that the total population of whiptails on the plot on that date ranged from 26–31 lizards. Lizard survey/transects and the lizard survey team were therefore fairly accurate in estimating the true whiptail populations on the study plot. Thus the number of lizards found on other transects in similar habitats may be used to estimate population numbers. Whiptails, of course, were not found on all transects due to habitat characteristics, low population numbers, or absence. Transect data and the Mott Reserve data show that when whiptails are present (1–4 lizards per 10 × 100 meters × 10 to equal 1 Ha) there are 10–40 whiptails/hectare. This is similar to the 6–30/ha density given by Milstead (in Gehlbach 1993) for *Cnemidophorus tigris* from southern Texas. Whiptails occur primarily, but not exclusively, in Coastal Sage Scrub. As an attempt to estimate the order of magnitude of the minimal population number of whiptails in Southern California, I used the low estimate of Atwood (1992) of 250,000 acres (101,214 ha) of remaining Coastal Sage Scrub vegetation in Southern California multiplied by the lowest number (10) of whiptails per hectare to give a minimal estimate of 1,012,140 lizards. The higher number of 40 lizards/hectare gives an estimate of 4,048,560 lizards. Higher estimates of the amount of Coastal Sage Scrub vegetation (see Minnich 1983) and the inclusion of lizard habitat other than Coastal Sage Scrub (Table 3) would, of course, increase these numbers. The total area of the range of Orange-throated Whiptails in California is calculated from Figures 1 and 5 as 2.5 million acres (1,012,145 ha). Using the low and high number for number of whiptails per hectare (10/40) times the area of the lizard's entire range in Southern California gives minimal and maximal estimates of numbers of whiptail lizards at 10 and 40 million. It is clear that whiptails are not present everywhere or equally throughout its range, nor even within Coastal Sage Scrub. However, they are present in altered and some urban areas. The function of these calculations, like those for elephants, rhinos, or gnatcatchers (Atwood, 1992) is to determine the order of magnitude of the number of whiptails in Southern California, so as to get a handle on its abundance or scarcity for conservation and legal protection purposes. Clearly, even if these whiptail numbers give over-estimates, they are over by a great many times the number needed to consider the species endangered.

Discussion

Concerns about habitat lost to a species are in fact related to loss of *preferred* habitat. The preferred habitat for Orange-throated Whiptails, based on this study is Coastal Sage Scrub (CSS) vegetation below 853m. But whiptails are also found in other habitats (Fig. 3). The percent of habitat lost to a species is usually calculated based on the amount of original vegetation of that type present. A critical question is, at what time does one start with the "amount of original vegetation." It is clear that much of the original pre-historic California Native Grassland and Coastal Sage Scrub vegetation was destroyed before 1900 (Atwood 1993; Cleland 1941, 1952; Keeley 1993). According to Atwood (1992) there was 1 million hectares of Coastal Sage Scrub in Southern California at the turn of the century with about 10% (or 100,000 hectares) of that remaining today in the southern four counties. The protected California Gnatcatcher, *Polioptila californica*, also occurs in Coastal Sage Scrub mostly below 608m, but in thicker vegetation than whiptails (Atwood 1988; Stine 1989). Unlike gnatcatchers, whiptails also enter other habitats (grassland; riparian and chaparral). Bird territories are large and roundish, with a pair of gnatcatchers needing about 20 acres of a territory (Atwood 1988, 1992, 1993). Whiptail home ranges are often elongate (Rowland 1992; Bostic 1965) and *much smaller*. Thus there can be more whiptails in a hectare of CSS in Southern California than California Gnatcatchers. Population numbers (Atwood 1992) of gnatcatchers are thus much lower (perhaps less than 4000 individuals: see Akcakaya and Atwood 1997) and far more potentially in danger of extinction than whiptails (Akcakaya and Atwood 1997). Whiptails also occur even in areas with some disturbance. The lizard needs some disturbance to form loose, coarse soil in which to burrow or lay eggs. Pre-historically those disturbances might have been made by large, now extinct, horses, camel, and bison. Historically they were probably made by Pronghorn Antelope and cattle (Cleland 1941, 1952). Today the disturbance comes from erosion, dirt roads, horse and hiking trails, and light ORV use.

Orange-throated Whiptail range and habitat occasionally overlaps with that of the state and federally protected Stephens' Kangaroo Rat, *Dipodomys stephensi.* While most of their habitat parameters are similar, whiptails prefer areas with loose, medium to coarse soil, and Stephens' Kangaroo Rats prefer areas with hard, yet fine-grained soil and a more restricted vegetation preference of Buckwheat, *Eriogonum fasciculatum*, Filaree, *Erodium*, and similar annuals (Stine 1989; O'Farrell and Uptain 1989; Price and Endo 1989; Burke, *et al* 1991).

Whiptails are present (verified in this study) within its preferred habitats in parts of all known designated Stephens' Kangaroo Rat Reserves (Stine 1989). While the California Gnatcatcher can fly, it is reluctant apparently to leave its tall, protective habitat (Atwood 1992). Stephens' Kangaroo Rat rapidly disperses into newly disturbed habitats (Price *et al* 1994; Brattstrom 1996). Orange-throated Whiptails can move in and out of habitat by direct movements and by dispersal, especially as related to its r-selected reproduction (Bostic 1996c; Rowland 1992) as shown for other species of *Cnemidophorus* (Walker and Cordes 1990). In 1990, I encountered an example of such movement into an area of a food resource. I was walking in a CSS Buchwheat habitat, in which I had seen whiptails, and entered an open area, devoid of Buckwheat. In this open area were many ground vines of the coastal Coyote Melon, *Curcurbita foetidissima.* The fruit of the vines include solid ripe green gourds as well as a few slightly dry gourds. Apparently coyotes had opened and eaten some of the gourds the previous several nights. As I walked over the vines, several whiptails ran out of the vine area and back over 30m of open, bare ground into the Buckwheat vegetation. Examination of the broken gourds revealed flies and fly larvae in and on the "meat" of the gourd. The whiptails apparently had left their preferred habitat, or wandered into the atypical habitat because of the temporary presence of appropriate food. Elsewhere, but in the same week, the two lizard survey personal, Dennis Strong and Brian Leatherman, observed the same phenomenon. Thus, while Coastal Sage Scrub may be the preferred vegetation type, they disperse widely and are found in many other vegetation types and in disturbed areas (Fig. 3).

Does the species, *Cnemidophorus hyperythrus*, meet the criteria for listing as a Threatened or Endangered Species? The criteria for listing a species for legal protection vary by public agency and, in practice, by the species of concern and the socio-political-economic problems associated with such listing. Mace and Lande (1991) have presented a proposed IUCN system of categories of legal protection with well defined criteria for each category. The categories are: EXTINCT, CRITICAL (50% probability of extinction within 5 years or 2 generations, whichever is longer), ENDANGERED (20% probability of extinction within 20 years or 10 generations, whichever is longer), VULNERABLE (10% probability of extinction within 100 years). These categories are further defined in terms of specific characteristics of the population biology of a species. California Gnatcatchers and Stephens' Kangaroo Rat both probably meet the endangered category (yet see Ludwig 1999). Based on the data collected in this study (whiptails present at 96% of all its known localities; r-selected reproduction, high local densities, high total numbers in its range), the Orange-throated Whiptail does *not* meet any of the present CDFG, State or Federal or proposed IUCN criteria. Therefore no recommendation for listing is made. Based on its abundance in preferred and even in some disturbed habitat, it may not deserve listing by any agency.

The greatest potential threat to this species is habitat loss. The best way to preserve or protect any species is to protect its habitat (Shafer 1991). About 40% of the range (overlays of maps in Figs. 1,5) of the whiptail is already protected in national forests, state and county parks, BLM land, and military bases including, Camp Pendelton, Fallbrook Naval Weapons Depot and Miramar Naval Air Station. Excluding certain areas reserved for military activity, all three of these bases have reserves or open spaces with Coastal Sage Scrub and with whiptails. These bases and the various government agencies have or are developing wildlife management plans, which include protection for all protected species including the Orange-throated Whiptail. The Riverside County Ordinance relating to Stephens' Kangaroo Rats (Stine 1989) defines specific areas called "study areas" for acquisition. These areas are good habitat for whiptails, and whiptails are known from each study area. Riverside County also has a functional Multispecies Habitat Conservation Plan which includes whiptails and locality data from this study. Orange County has only 15.4% of its land in public ownership, while the other counties in the range of the whiptail, have 47–53% of their land in State, Federal, County, City, or other public land ownership. This public ownership, in addition to private lands held for conservation purposes, provides potential habitat reserves for whiptails and other reptiles and amphibians.

There are many city and county parks and open space areas in Southern California. Many of these areas have whiptails. These areas may or may not be large enough for sustainable lizard populations and most of these areas are under local management and therefore come upon many local socio-political-economic pressures. For example, whiptails occur in the City of Anaheim's Oak Canyon Nature Area. This park has a nature-preservation-no-collecting orientation and whiptails continue to survive in this nature area. However, the City of Anaheim also has a policy of building on all surrounding hills until it meets the Irvine Company land to the east. The latter also has a prodevelopment policy. Yet, recent (1997–1999) political, environmental pressure has forced these two cities to provide more and more open space. The question is, of course, how long can this or any other small isolated population (Akcakaya and Atwood 1997) survive? It is clear that whiptails can persist on some small areas. Whiptails were first collected on the U.S. Navy property at the tip of Point Loma, San Diego County in 1893, and that population, even though surrounded by water and the City of San Diego, still persists today. In any event, general principles of biogeography (Shafer 1991) would suggest that it is wiser to enlarge an already large habitat area than to expand by a few acres a small area already surrounded by development. Lands in public ownership (for whiptails especially, this includes BLM, U.S. Forest Service, State Parks) and private environmental agencies (Nature Conservancy) will provide, hopefully, important protected areas for Orange-throated Whiptails. On a personal note, in 1999, it is gratifying to see that lizard reserve recommendations made in 1990–1993 to various agencies and environmental groups have resulted in the establishment or the expansion of numerous reserves that specifically protect habitat for Stephens' Kangaroo Rat, California Gnatcatcher, and the Orange-throated Whiptail.

Acknowledgments

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In order to carry out this study it was necessary to develop a team. My team of CSUF graduate and undergraduate students included; Victor Horchar, data analyzer, GIS analyzer, purchasing agent, gopher and all around problem-solver; Scott Rowland and Steve Hager, who did their Master's degree theses on the population ecology, activity, home range, etc. of the whiptail and horned lizard respectively; For field surveys, I needed two good "lizard chasers" and I found them in Dennis Strong and Brian Leatherman. Tania Marien had the task of learning all that she could about termites (the main food of the whiptail) and then teaching the rest of us what she learned. In the process she carried out many experiments on ants and termites. Mary Hack-Stover was in charge of managing the bibliographic material. Michele Garden did experiments on soil size choice.

A large number of people were contacted during the course of this study, and a large number of persons or agencies contacted us. Many of these people provided information, ideas, or references, while others had informational requests of me. The complete list of people, to whom I owe my thanks, is provided in Brattstrom (1993).

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Ants (Hymenoptera: Formicidae) of Santa Cruz Island, California

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Abstract.—We conducted ant surveys on Santa Cruz Island, the largest of the California Channel Islands, in 1975/6, 1984, 1993, and 1998. Our surveys yielded a combined total of 34 different ant species: *Brachymyrmex* cf. *depilis, Camponotus anthrax, C. clarithorax, C. hyatti, C. semitestaceus, C. vicinus, C.* sp. near *vicinus, C. yogi, Cardiocondyla ectopia, Crematogaster californica, C. hespera, C. marioni, C. mormonum, Dorymyrmex bicolor, D. insanus* (s.l.), *Formica lasioides, F. moki, Hypoponera opacior, Leptothorax andrei, L. nevadensis, Linepithema humile, Messor chamberlini, Monomorium ergatogyna, Pheidole californica, P. hyatti, Pogonomyrmex subdentatus, Polyergus* sp., *Prenolepis imparis, Pseudomyrmex apache, Solenopsis molesta* (s.l.), *Stenamma diecki, S. snellingi, S.* cf. *diecki*, and *Tapinoma sessile*. The ant species form a substantial subset of the mainland California ant fauna. We found only two ant species that are not native to North America, *C. ectopia* and *L. humile. Linepithema humile*, the Argentine ant, is a destructive tramp ant that poses a serious threat to native ants.

The California Channel Islands lie in the Pacific Ocean, 20 to 100 km off the coast of southern California. As a result of isolation from the mainland, many endemic plant and animal species have evolved on these islands (Wenner and Johnson 1980; Diamond and Jones 1980; Nagano et al. 1983; Junak et al. 1995), including more than 100 species of endemic insects (Miller 1985). Two ant species, *Aphaenogaster patruelis* Forel and *Camponotus bakeri* Wheeler, are recognized as endemic to the Channel Islands (Miller 1985).

Santa Cruz Island (SCI) is the largest (245 km^2) of the Channel Islands. In the past, SCI was used for ranching of cattle, sheep, and horses, as well as some agriculture and tourism (Junak et al. 1995). There were also several military installations. SCI is now entirely a nature reserve, with a resident human population of fewer than twenty people. One small, largely unmanned U.S. Navy installation remains. The western 90% of the island is owned by The Nature Conservancy, a private conservation organization, and the eastern 10% is part of

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Table 1. Ant species recorded on Santa Cruz Island. Pub = previous records (see Introduction). * = unpublished record (see Results). T75/6 = Trager and Trager surveys in 1975/6. L84 = Longino survey in 1984. PW93 = Ward et al. survey in 1993. JW98 = Wetterer et al. survey in 1998. X = found in survey.

Species	Survey				
	Pub	T75/6	L84	PW93	JW98
Brachymyrmex cf. *depilis*					X
Camponotus anthrax Wheeler	X	X			
Camponotus clarithorax Emery		X	X	X	X
Camponotus hyatti Emery		X	X	X	X
Camponotus semitestaceus Snelling		X	X	X	X
Camponotus vicinus Mayr			X		
Camponotus sp. near *vicinus*	X	X	X	X	X
Camponotus yogi Wheeler			X	X	
Cardiocondyla ectopia Snelling					X
Crematogaster californica Wheeler				X	
Crematogaster hespera Buren			X	X	
Crematogaster marioni Buren		X	X	X	X
Crematogaster mormonum Wheeler	X	X			
Dorymyrmex bicolor Wheeler		X	X	X	X
Dorymyrmex insanus (Buckley) (s.l.)		X	X	X	X
Formica lasioides Emery		X			
Formica moki Wheeler	X	X	X	X	X
Hypoponera opacior (Forel)		X	X	X	X
Leptothorax andrei Emery		X	X	X	X
Leptothorax nevadensis Wheeler	*	X			
Linepithema humile (Mayr)					X
Messor chamberlini Wheeler	X			X	X
Monomorium ergatogyna Wheeler	X		X	X	X
Pheidole californica Mayr	X	X	X	X	X
Pheidole hyatti Emery	X	X	X	X	X
Pogonomyrmex subdentatus Mayr					X
Polyergus sp.		X		X	X
Prenolepis imparis (Say)	X	X	X		X
Pseudomyrmex apache Creighton	X	X		X	X
Solenopsis molesta Say (s.l.)		X	X	X	X
Stenamma diecki Emery			X	X	
Stenamma snellingi Bolton				X	
Stenamma cf. *diecki*				X	
Tapinoma sessile (Say)		X	X	X	X
# of species	10	21	20	24	23
# not recorded in earlier surveys		13	4	3	4

Channel Islands National Park. The island is far from pristine, with large populations of exotic plants (e.g., fennel, *Foeniculum vulgare* Miller) and animals (e.g., feral pigs, *Sus scrofa* L.) (Junak et al. 1995).

The California Channel Islands remain poorly studied by biologists. There have been no published comprehensive ant surveys of any of the California Channel Islands, and we found few published records of ants from SCI. Earlier published records noted only 10 different ant species on SCI (Table 1). Wheeler (1915) described *Messor chamberlini* Wheeler from SCI and also recorded *Pheidole californica* Mayr. Fall and Davis (1934) collected *Pheidole hyatti* Emery on SCI, incidental to their study of the island's beetles. Mallis (1941) added *Prenolepis imparis* (Say), *Camponotus* sp. near *vicinus* (as *Camponotus sansabeanus vicinus* var. *maritimus*), and *Formica moki* Wheeler (as *Formica rufibarbis* var. *occidua*) to the list. More recent ant records from SCI include additional *Formica moki* (Francoeur 1973; Francoeur and Snelling 1979), as well as *Crematogaster mormonum* Wheeler (Rentz and Weissman 1981), *Pseudomyrmex apache* Creighton (Ward 1985), *Monomorium ergatogyna* Wheeler (Dubois 1986), and *Camponotus anthrax* Wheeler (Snelling 1988).

From the published records of only 10 ant species known from SCI, one might conclude that the diversity of ant fauna of this island is quite impoverished compared to the ant fauna of mainland California sites, where ant surveys typically collect more than 20 ant species (see Discussion). However, we present the results of four ant surveys conducted on SCI in 1975/6, 1984, 1993, and 1998, which greatly expand the known species list for SCI. This present synthesis was prompted by the discovery on SCI of the Argentine ant, *Linepithema humile*, a highly destructive tramp ant that poses a serious threat to native ants. Adrian Wenner first found *L. humile* on SCI in January 1996. A follow-up study by Andrew Calderwood and Emily Hebard in July 1997 found that *L. humile* occupied two noncontiguous areas, surrounding two dismantled Navy support facilities, that totaled less than 1% of the island (Calderwood et al. 1999).

Methods

In the fall of 1975, G. Trager surveyed ants on Santa Cruz Island using hand-collecting. In the summer of 1976, G. Trager and J. Trager further surveyed SCI ants using hand-collecting and tuna bait transects. J. Trager identified the ants from 1975/6. Vouchers are in the personal collection of G. Trager and unavailable for this study. From 24–27 August 1984 and 26–29 October 1984, J. Longino surveyed SCI ants using hand-collecting. Longino identified these ants and placed vouchers in the Natural History Museum of Los Angeles County (LACM) and the University of California (UC) Field Station on Santa Cruz Island. On 25–28 June 1993, P. Ward, B. Fisher, and M. Bennett surveyed SCI ants using hand-collecting and Winkler litter sifting. Ward identified the ants and placed vouchers in the Bohart Museum of Entomology, University of California, Davis, and duplicates at the LACM and the Museum of Comparative Zoology at Harvard University (MCZ). Finally, in March–May 1998, J. Wetterer, A. Wetterer, A. Wenner, A. Calderwood, and E. Hebard surveyed ants (with the assistance of numerous volunteers, primarily undergraduate students studying at Biosphere 2 Center), using hand-collecting, bait transects (with tuna and Pecan Sandies cookies as bait), and litter samples in Berlese funnels. S. Cover at the MCZ and P. S. Ward identified these ants. We have placed voucher specimens in the MCZ.

Results

Each of the four surveys of Santa Cruz Island yielded 20 to 24 ant species (Table 1). Altogether, a total of 34 different ant species were recorded by our surveys, including all 10 previously recorded species (Table 1). All 34 species are known from mainland California. Only 13 ant species were found in all four surveys, and only four of these had been previously recorded from SCI. Each of the surveys yielded at least three ant species not recorded in any earlier survey

(Table 1). None of the surveys collected either of the two endemic Channel Island ant species.

There are a number of taxonomic problems concerning the ants of SCI. Two ants, *Dorymyrmex insanus* (Buckley) (s.l.) and *Solenopsis molesta* Say (s.l.), belong to species-groups whose species boundaries have not been adequately defined (S. Cover, personal communication). Several researchers first identified the *Polyergus* specimens from SCI as *Polyergus breviceps* Emery. However, Trager (personal observation) determined the specimens to be an undescribed species with physical proportions quite distinct from *P. breviceps*. This undescribed species is unique to southern California and parasitizes only *F. moki*. We were unable to identify with certainty two ant species, listed as *Brachymyrmex* cf. *depilis* and *Stenamma* cf. *diecki*.

Cover and Longino identified *Camponotus* sp. near *vicinus* as the ant Wheeler (1910) described as *Camponotus maculatus vicinus* var. *maritimus* Wheeler, but this ant was referred to *Camponotus vicinus* Mayr by Creighton (1950). Both *Camponotus vicinus* and *Camponotus* sp. near *vicinus* occurred on SCI where they are distinct and appear to represent separate species. *Camponotus* sp. near *vicinus* was very common on SCI, whereas true *C. vicinus* was rare. In 1984, Longino found only one nest of true *C. vicinus*, under dead wood in the pine stand on the east end of SCI. In contrast, Longino (personal observation) found that *Camponotus* sp. near *vicinus* was rare in the chaparral around Santa Barbara on the adjacent mainland California, where true *vicinus* was common. Longino examined all *C. vicinus* and *C.* sp. near *vicinus* specimens at the Los Angeles County Museum, and concluded that some specimens from farther south in California were apparently intermediate between the two forms. In northern California, the two species are consistently distinct and recognizable (Ward, personal observation).

Camponotus hyatti Emery is quite variable on SCI, in some cases approaching the morphology of the closely related species *Camponotus bakeri* Wheeler. *Camponotus bakeri* is currently recognized as endemic to the southern Channel Islands of Santa Catalina, San Clemente, and Santa Barbara (Snelling 1988), but the relationship and distribution of *C. hyatti* and *C. bakeri* need critical review.

Longino (personal observation) identified a single damaged and undated specimen in the collection of the UC Field Station on SCI as belonging to the *Leptothorax nevadensis* Wheeler group, corroborating the 1975/76 record of *L. nevadensis*. Two species recorded in the 1975/76 survey (*Camponotus dumetorum* Wheeler and *Camponotus sayi* Emery) are excluded because identifications of the specimens are uncertain and no vouchers are available. *Crematogaster mormonum*, also recorded in an earlier study (Rentz and Weissman 1981), warrants confirmation, as it is easy to misidentify this species.

Cardiocondyla ectopia Snelling and *Linepithema humile* (Mayr) are the only ant species we found on SCI known to be not native to North America. We collected *Cardiocondyla ectopia*, an Old World species (Snelling 1974), only around buildings of the Stanton Ranch, currently used as the island headquarters of The Nature Conservancy. Our 1998 survey confirmed the distribution of *L. humile* documented (see map in Calderwood et al. 1999) and failed to locate any additional *L. humile* populations on the island.

Discussion

The number of ant species found in our surveys of Santa Cruz Island was similar to ant surveys on mainland California. For example, Fisher (1997) surveyed eight sites in northern California and found a total of 27 different ant species. Holway (1998) surveyed a similar northern California area and found 26 ant species. Suarez et al. (1998) surveyed 47 sites in southern California and found a total of 50 different ant species.

The ant species of SCI form a substantial subset of the mainland California ant fauna (Ward 1987, Fisher 1997; Holway 1998; Suarez et al. 1998; Ward, unpublished). Many common mainland ant species, however, were not found on SCI, including *Camponotus essigi* Smith, *Liometopum occidentale* Emery, *Neivamyrmex californicus* (Mayr), *N. nigrescens* (Cresson), *Formica francoeuri* Bolton, *Leptothorax nitens* Emery, *Messor andrei* (Mayr), *Pogonomyrmex californicus* (Buckley), and *Solenopsis xyloni* McCook (Ward 1987; Fisher 1997; Human and Gordon 1997; Holway 1998; Suarez et al. 1998).

The ocean appears to have been an effective barrier to colonization of SCI by many ants common on mainland California. It is unclear how many of the ant species now on SCI predate human habitation on the island. The two exotic ant species, *Cardiocondyla ectopia* and *Linepithema humile*, almost certainly arrived on SCI through human activity. We found both species only surrounding building sites.

The arrival of *Linepithema humile* on SCI is particularly distressing. Originally from South America and commonly called the Argentine ant, this ant is now a pest in subtropical and temperate regions around the world, including Australia (Majer 1994), South Africa (Hattingh 1945), the Middle East (Tigar et al. 1997), southern Europe (Way et al. 1997), Bermuda (Hilburn et al. 1990), the southern mainland United States (Barber 1916), and Hawaii (Reimer et al. 1990; Wetterer 1998; Wetterer et al. 1998). *Linepithema humile* first arrived in California earlier this century and has steadily spread across the state (Ward 1987; Holway 1995; Human and Gordon 1997). *Linepithema humile* has become the most common pest ant in urban areas of California (Knight and Rust 1990).

In areas where *L. humile* invades, native invertebrate species are heavily impacted (Erickson 1971; Cole et al. 1992; Ward 1987; Human and Gordon 1997; Way et al. 1997; Holway 1998; Suarez et al. 1998). This is true on SCI as well. Within the two areas that *L. humile* has invaded, only two other ant species have persisted, *Monomorium ergatogyna* and *Solenopsis molesta* (Wetterer et al., unpublished data). Elsewhere on SCI, the native ant fauna appears to be fairly intact. The previous absence of destructive exotic ants on SCI has likely permitted many species of native invertebrates to persist. However, if *L. humile* spreads, these native species may be seriously threatened.

Linepithema humile is also known from two other California Channel Islands. This ant is established on Santa Catalina Island (Cockerell 1940; Rentz and Weissman 1981), the only Channel Island with a sizable human population. There is also one record of *L. humile* from San Clemente Island (Straughan 1982). Comprehensive ant surveys are needed on these and the other California Channel Islands to evaluate the distribution and impact of *L. humile* and to determine what, if anything, should be done to curtail its spread.

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Has Point Conception been a Marine Zoogeographic Boundary throughout the Holocene? Evidence from the Archaeological Record

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Abstract.—Fish remains recovered from archaeological sites along the California coast to the immediate north and south of Pt. Conception in San Luis Obispo and Santa Barbara counties are used to test the hypothesis that the ranges of marine fishes have remained constant during the Holocene. The archaeological record shows that as many as 16 species are only found in locations south of Pt. Conception and as many as eight are found only to the north. These prehistoric ranges are consistent with their present ranges.

Currently, Pt. Conception is the northern extent of the range of many southern California marine fish species, and the approximate southern extent of central and northern California marine fishes (Eschmeyer et al. 1983). This investigation tests whether or not the archaeological record of fish remains reflects this zoogeographical boundary role. In this survey, the results of the evaluations of fish materials from numerous archaeological sites in San Luis Obispo County, north of Pt. Conception, (many of which have been reported by Gobalet and Jones 1995), are compared with numerous sites in Santa Barbara County south of Pt. Conception (Figure 1). These archaeological sites are particularly suitable for this study because they were all occupied by a single ethnic group of Native Americans, the Chumash (Holmes and Johnson 1998). The presence of this common culture should minimize any bias for fish capture or consumption, although as one goes back in time this assumption becomes problematic.

The 12 archaeological sites reported by Gobalet and Jones (1995) were occupied at various times from 6200 BC to AD 1830. Archaeological site SLO-1796 is even older, at approximately 8300 to 7500 BC (T. Jones, personal communication). Three Santa Barbara archaeological sites (SBA-1807, -2057, -2061) reported by Erlandson (1994) and SBA-1 were occupied within the range of 9000–5000 BC with SBA-1 additionally yielding a date of approximately 800 BC (Erlandson 1991). The five sites (SBA-71, -72, -73, -1674, and -1731) on which Johnson worked (Table 2) were variously occupied from the first century AD to AD 1300 (J. Johnson personal communication) and SBA -3404 at a later time from AD1100–1804 (W. Hildebrandt, personal communication).

In a study of over 77,000 remains from 51 archaeological sites from the central California coast, Gobalet and Jones (1995) concluded that the fishery resources were locally derived. As a consequence, the archaeological record for coastal sites should reflect the resources immediately available. The same can not be said of inland localities where numerous marine species were transported considerable

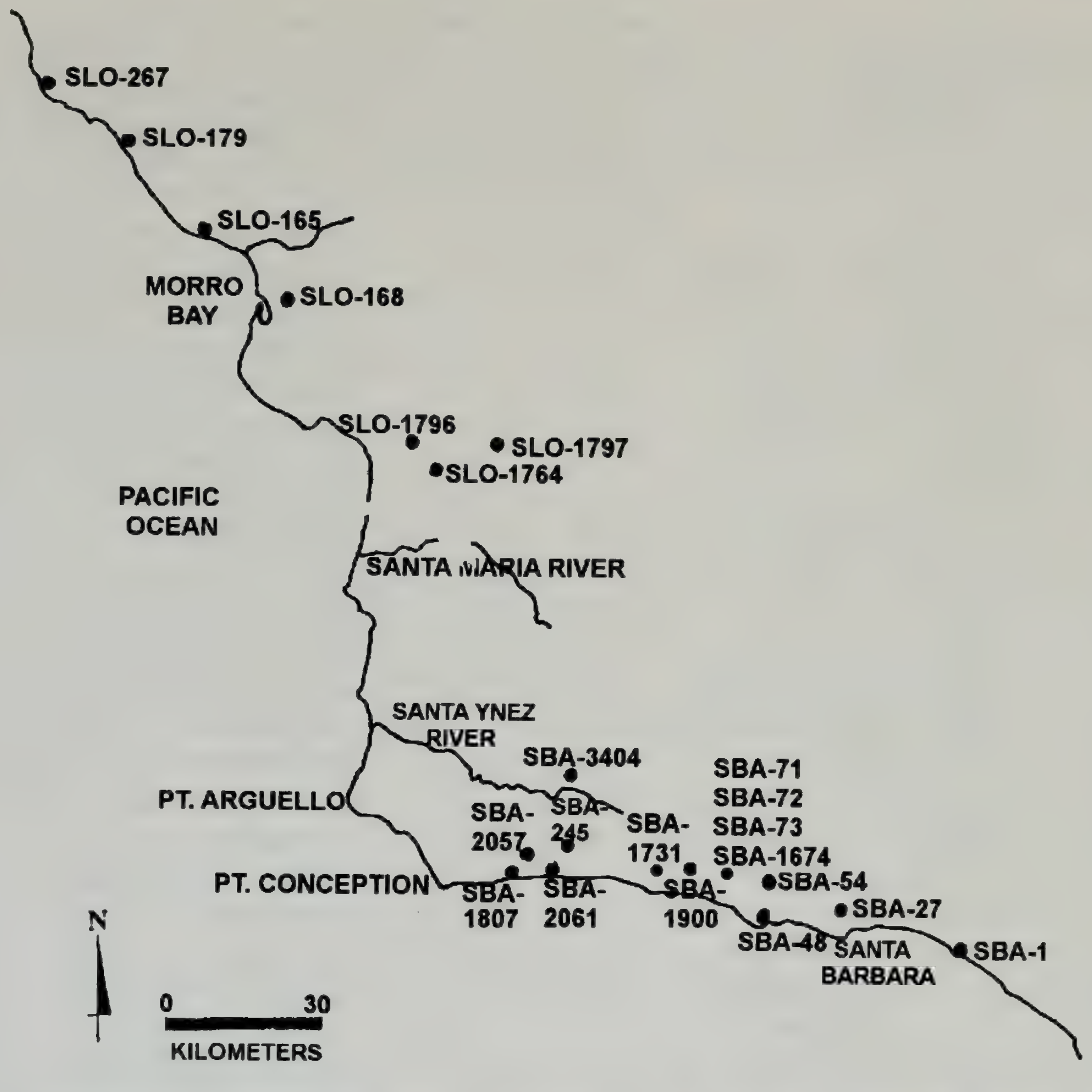
SLO-267
SLO-179
SLO-165
MORRO BAY
SLO-168
SLO-1796
SLO-1797
SLO-1764
PACIFIC OCEAN
SANTA MARIA RIVER
SANTA YNEZ RIVER
SBA-3404
PT. ARGUELLO
SBA-2057
SBA-245
SBA-1731
SBA-71
SBA-72
SBA-73
SBA-1674
PT. CONCEPTION
SBA-1807
SBA-2061
SBA-1900
SBA-54
SBA-27
SBA-48
SANTA BARBARA
SBA-1
N
0
30
KILOMETERS

Fig. 1. Location of archaeological sites considered in this paper in San Luis Obispo and Santa Barbara Counties.

distances (Gobalet 1992) or in some freshwater localities, where the archaeological record has been used to expand known historic ranges (Gobalet 1990; 1993).

Though most of the fish species found at sites in San Luis Obispo and Santa Barbara Counties range to the north or south of Pt. Conception, many can be used to test the hypothesis that the archaeological record reflects that Pt. Conception had the same boundary role for these species prior to European contact as found in subsequent historic surveys of aquatic biota. Fishes found at the archaeological sites under consideration (Table 1) that are generally restricted to waters south (east) of Pt. Conception include: horn shark, shortfin mako shark, swell shark, gray smoothhound, California scorpionfish, kelp bass, Pacific barracuda, California sheephead, sargo, salema, opaleye, blacksmith, giant seabass, white seabass, California corbina, yellowfin croaker, black croaker, queenfish, and rock wrasse (Miller and Lea 1972, Eschmeyer et al. 1983). Species generally restricted to marine waters north of Pt. Conception that have been recovered from archaeological sites in San Luis Obispo and Santa Barbara Counties include: night smelt, northern clingfish, kelp greenling, monkeyface prickleback, rock prickleback, crevice kelpfish, and Pacific tomcod (Miller and Lea 1972, Eschmeyer et al. 1983). For the prediction to be supported, the species indicated north of Pt. Conception should primarily be found in the San Luis Obispo County archaeological sites and not in the Santa Barbara County sites, and the reverse should be true for the species found south of Pt. Conception.

Table 1. List of scientific and common names of fishes used in this paper. Terminology and order of presentation follow Robins et al. (1991).

Scientific name	Common name
Elasmobranchiomorphii	
Hexanchidae	cow sharks
Notorynchus cepedianus	sevengill shark
Cetorhinidae	basking sharks
Cetorhinus maximus	basking shark
Heterodontidae	bullhead sharks
Heterodontus francisci	horn shark
Lamnidae	mackerel sharks
Carcharodon carcharias	white shark
Isurus oxyrinchus	shortfin mako
Lamna ditropis	salmon shark
Alopiidae	thresher sharks
Alopias vulpinus	thresher shark
Scyliorhinidae	cat sharks
Cephaloscyllium ventriosum	swell shark
Carcharhinidae	requiem sharks
Carcharhinus brachyurus	narrowtooth shark
C. leucas	bull shark
C. longimanus	oceanic whitetip shark
C. obscurus	dusky shark
Galeocerdo cuvier	tiger shark
Galeorhinus zyopterus	soupfin shark
Mustelus californicus	gray smoothound
M. henleyi	brown smoothound
M. lunulatus	sicklefin smoothound
Prionace glauca	blue shark
Rhizoprionodon longurio	Pacific sharpnose shark
Triakis semifasciata	leopard shark
Squalidae	dog fish sharks
Squalus acanthias	spiny dogfish
Squatinidae	angel sharks
Squatina californica	angel shark
Rhinobatidae	guitarfishes
Platyrhinoidis triseriata	thornback
Rhinobatos productus	shovelnose guitarfish
Rajidae	skates
Raja binoculata	big skate
R. inornata	California skate
Dasyatidae	stingrays
Dasyatis dipterura	diamond stringray
Urolophidae	round stingrays
Myliobatidae	eagle rays
Myliobatis californica	bat ray
Actinopterygii	
Clupeidae	herrings
Clupea pallasi	Pacific herring
Sardinops sagax	Pacific sardine
Engraulidae	anchovies
Engraulis mordax	northern anchovy
Osmeridae	smelts
Spirinchus starksi	night smelt

Table 1. Continued.

Scientific name	Common name
Salmonidae	trouts
Oncorhynchus mykiss	steelhead (anadromous rainbow trout)
Ophiidae	cusk eels
Chilara taylori	spotted cusk eel
Gadidae	cods
Merluccius productus	Pacific hake
Microgadus proximus	Pacific tomcod
Batrachoididae	toadfishes
Porichthys spp.	specklefin and plainfin midshipman
Gobiesocidae	clingfishes
Gobiesox meandricus	northern clingfish
Atherinidae	silversides
Atherinops affinis	topsmelt
Atherinopsis californiensis	jacksmelt
Leuresthes tenuis	California grunion
Gasterosteidae	sticklebacks
Gasterosteus aculeatus	threespine stickleback
Scorpaenidae	scorpionfishes
Scorpaena guttata	California scorpionfish
Sebastes spp.	rockfishes
S. auriculatus	brown rockfish
S. carnatus	gopher rockfish
S. diploproa	splitnose rockfish
S. goodei	chilipepper
S. miniatus	vermillion rockfish
S. paucispinis	bocaccio
S. rastrelliger	grass rockfish
S. serriceps	treefish
Hexigrammidae	greenlings
Hexagrammos decagrammus	kelp greenling
H. lagocephalus	rock greenling
Ophiodon elongatus	lingcod
Cottidae	sculpins
Clinocottus analis	woolly sculpin
Hemilepidotus spinosus	brown Irish lord
Leptocottus armatus	Pacific staghorn sculpin
Scorpaenichthys marmoratus	cabezon
Percichthyidae	temperate basses
Steriolepis gigas	giant seabass
Serranidae	sea basses
Paralabrax clathratus	kelp bass
P. maculatofasciatus	spotted sandbass
P. nebulifer	barred sandbass
Carangidae	jacks
Seriola lalandi	yellowtail
Trachurus symmetricus	jack mackerel
Anisotremus davidsoni	sargo
Xenistius californiensis	salema
Sciaenidae	drums
Atractoscion nobilis	white seabass
Cheilotrema saturum	black croaker
Genyonemus lineatus	*white croaker*
Menticirrhus undulatus	*california corbina*

Table 1. Continued.

Scientific name	Common name
Seriphus politus	queenfish
Umbrina roncador	yellowfin croaker
Kyphosidae	sea chubs
Girella nigricans	opaleye
Embiotocidae	surfperches
Amphistichus sp.	barred, calico, or redtail surfperch
Brachyistius frenatus	kelp perch
Cymatogaster aggregata	shiner perch
Embiotoca jacksoni	black perch
E. lateralis	striped surfperch
Hyperprosopon argenteum	walleye surfperch
H. anale	spotfin surfperch
Hypsurus caryi	rainbow seaperch
Micrometrus sp.	reef or dwarf surfperch
Phanerodon furcatus	white seaperch
Rhacochilus toxotes	rubberlip seaperch
R. vacca	pile perch
Pomacentridae	damselfishes
Chromis punctipinnis	blacksmith
Sphyraenidae	barracudas
Sphyraena argentea	Pacific barracuda
Labridae	wrasses
Halichoeres semicinctus	rock wrasse
Semicossyphus pulcher	California sheephead
Stichaeidae	pricklebacks
Cebidichthys violaceus	monkeyface prickleback
Plagiogrammus hopkinsi	crisscross rickleback
Xiphister mucosus	rock prickleback
Pholidae	gunnels
Apodichthys flavidus	penpoint gunnel
Anarhichadidae	wolffishes
Anarrhichthys ocellatus	wolf-eel
Clinidae	clinids
Gibbonsia montereyensis	crevice kelpfish
Heterostichus rostratus	giant kelpfish
Gobiidae	gobies
Eucyclogobius newberryi	tidewater goby
Gillichthys mirabilis	longjaw mudsucker
Scombridae	mackerels
Sarda chiliensis	Pacific bonito
Scomber japonicus	chub mackerel
Thunnus alalunga	albacore
Xiphiidae	swordfishes
Xiphias gladius	swordfish
Bothidae	lefteye flounders
Citharichthys sp.	sanddabs
Paralichthys californicus	California halibut
Pleuronectidae	righteye flounders
Atherestes stomias	arrowtooth flounder
Hypsopsetta guttulata	diamond turbot
Platichthys stellatus	starry flounder
Pleuronichthys coenosus	C-O sole
P. ritteri	spotted turbot

Methods

Common and scientific names follow Robins et al. (1991) (Table 1). Original identifications in this study were made by comparison with skeletal materials at the Department of Biology, California State University, Bakersfield, and the Museum of Natural History of Los Angeles County. The lowest possible taxon was determined except where discrimination was not useful or exceedingly time consuming. For example, distinguishing between the 59 ecologically and morphologically similar species of rockfishes (Lea 1992) is judged unlikely, especially when identification is based on vertebrae and fragmentary skeletal materials (Gobalet and Jones 1995). Therefore, identifications within the genus *Sebastes* are reported as rockfishes. The reports of findings of rockfish species of other authors, however, are included for completeness, but are viewed with suspicion. The kelp greenling was chosen over the rock greenling on the basis of their ranges (Eschmeyer et al. 1983). Within the genera *Raja* (skates), *Porichthys* (plainfin and specklefin midshipman) and *Paralabrax* (kelp, spotted, and barred sandbasses), the inability to discriminate between species prohibited further identification. With the exception of the chub mackerel and Pacific bonito, discrimination between mackerels (family Scombridae) was limited because of the shortage of comparative materials. Certain elements are diagnostic for requiem sharks (family Carcharhinidae); rays (order Rajiformes); Pacific sardine and Pacific herring (family Clupeidae); topsmelt, jacksmelt, and California grunion (family Atherinidae); surfperches (family Embiotocidae); clinids (family Clinidae); gobies (family Gobiidae); and numerous righteye and lefteye flounders (families Bothidae and Pleuronectidae). However, the broader groups were used because attempting to achieve species identifications using the most commonly recovered elements, vertebrae, for ray-fined fishes and centra for elasmobranchs, can be extremely time-consuming or impossible. Some appropriate comparative materials were not available. It is important that identifications be corroborated by more than one investigator because of dramatic discrepancies in interpretation by specialists (Gobalet unpublished data).

Results and Discussion

Published data from 12 sites in San Luis Obispo County, and unpublished data from three of these sites (SLO-165, -267, -179), as well as four additional sites (SLO-168, -1764, 1796, 1797) are included in Table 2. Table 2 also contains published data from four sites in Santa Barbara County (SBA-1, SBA-1807, -2057, and -2061,) along with unpublished data from 11 different sites and additional data for SBA-1 (Peterson 1984). In general, these data reflect that Pt. Conception has been a consistent zoogeographic barrier for the duration of human exploitation of the marine resources.

Horn shark remains have been found by separate investigators at sites in Santa Barbara County south of Pt. Conception. Because the four unstipulated elements attributed to horn shark by Salls et al. (1989, in Gobalet and Jones 1995) have not been reinforced by findings in two subsequent studies of SLO-165, the data are considered unconfirmed. Both shortfin mako (5 elements) and swell shark (3 elements) have been found by independent investigators only in southern California locations and not to the north. The abundance of true smelt (most likely night smelt), family Osmeridae, found at several sites exclusively in San Luis

Table 2. Number of Fish Remains from Archeological Sites in Santa Barbara and San Luis Obispo Counties.

	Archaeological Site														
Species	SLO[a] (12 sites)	SLO[b] -165	SLO -267	SLO[C] -179	SLO 168	SLO[d] -1764, -1796	SLO subtotal	SBA[e] -54	SBA -3404	SBA[f] -245	SBA[g] -1	Salls[h] (3 sites)	Johnson[i] (5 sites)	Erlandson[j] (3 sites)	SBA Subtotal
Elasobranchiomorphi	113	29		6		1	149	545	2	8	19	11	20	14	619
Horn shark	4						4	6			5				11
White shark										1	3				4
Shortfin mako shark								1		1	4	4	1	10	21
Swell shark								1			4		4		9
Requiem sharks	183	152	2	37			374	26	4		6	11			47
Soupfin shark								54			17	53	6		130
Grey smoothound	3	1					4				2	21			23
Blue shark	1						1				1	14	1		16
Leopard shark	3	4					7				3	50			53
Spiny dogfish	15			5			20	13			25	1			39
Angel shark	10	2					12	11			374	10			395
Rajiformes	25	2		12			39	194							194
Thornback	37	2		3			42	137				99		20	256
Shovelnose guitarfish	65	25					90	60			10	345		3	418
Raja sp.								50			13				63
Round stingray	1						1					1		1	2
Bat ray	208	96				1	305	39	2		57	52	2	35	187
Herrings	1362	46	129	1886	1	116	3540	446	1530	4	697	448	451	403	4047
Northern anchovy	542	27	24	619			1212	1	512		148	3		1	665
Smelts, inc. night smelt	126	3	3	568	1		701								
Steelhead	8			16			24	1	6					1	7
Pacific tomcod	2						2								
Pacific hake	44	3		1			48								
Porichthys sp.					1		1	52							52
Plainfin midshipman	49	2		6			57	1			1	12		2	13
Northern clingfish	9		9	3			21								
Silversides	1146	56	33	280	4	24	1543	54	6	5	14		6		7
Threespine stickleback	4					1	5								

Table 2. Continued.

Species	SLO[a] (12 sites)	SLO[b] -165	SLO -267	SLO[C] -179	SLO 168	SLO[d] -1764, -1796	SLO subtotal	SBA[e] -54	SBA -3404	SBA[f] -245	SBA[g] -1	Salls[h] (3 sites)	Johnson[i] (5 sites)	Erlandson[j] (3 sites)	SBA Subtotal
	Archaeological Site														
California scorpionfish												7			7
Rockfishes	1736	15	460	2031	2	8	4252	73	159	25	19	41	58	3	378
Kelp greenling	79	1	71	96			247	3	3			1			7
Lingcod	59	9	3	33			104					27	2		29
Sculpins	21		3	5			29							1	1
Pacific staghorn sculpin	263	12					275					5			5
Cabezon	273	16	75	540			904	7	1	1					9
Giant seabass											1				1
Paralabrax sp.	1						1	2	1			32	4		39
Yellowtail	1						1				2		1	1	4
Jack mackerel	4			6			10	16	5		1	100	6		128
Drums	6			2			8	3	13			11			27
White seabass											2	12			14
California corbina												10			10
Yellowfin croaker												10			10
Black croaker												3			3
White croaker	8			1			9	36	5		1197	265	29	12	1544
Queenfish	1			7			8	230	2		42	13		5	292
Surfperches	1274	63	149	613	7	2	2108	202	35	10	308	32	39	22	648
Amphistichus sp.	7		1	10			18			1	1	4			6
Shiner perch	59	1		2	2		64				2	46	89		137
Embiotoca sp.	7		4	27	1		39								
Black perch				2			2					11	28	1	40
Walleye surfperch	21			1			22				3	12	18		33
Micrometrus sp.	1				1		2							1	1
White seaperch											5	125	27		157
Rubberlip seaperch	11				1		12					24	1		25
Pile perch	258	4	58	81			403	13			70	375	20	13	491
Pacific barracuda	1			1	2	2	60	2		6	23	1	1	1	93

Table 2. Continued.

Species	Archaeological Site														
	SLO[a] (12 sites)	SLO[b] -165	SLO -267	SLO[c] -179	SLO 168	SLO[d] -1764, -1796	SLO subtotal	SBA[e] -54	SBA -3404	SBA[f] -245	SBA[g] -1	Salls[h] (3 sites)	Johnson[i] (5 sites)	Erlandson[j] (3 sites)	SBA Subtotal
Señorita	61		2	15			79		10		51		31		92
California sheephead						1		31		1	2	14		1	49
Rock wrasse												1			1
Blacksmith	7						7					25			25
Pricklebacks	7		360				367								
Monkeyface prickleback	289	3	45	185			522								
Rock prickleback	67		101	43		1	212								
Clinids	1		1	15			17	2							2
Gibbonsia	13		7	10			30								
Giant kelpfish	3		3	4	2		12					1			1
Mackerels								42	13						55
Pacific bonito									1		34	77	2		114
Chub mackerel	3		4				7	214	138	2	21	36	24		435
Lefteye and righteye flounders	5	2		1			8	9	1						10
California halibut	3						3		1		1	44			46
Starry flounder	6			1			7								
Total	8788	577	1547	7176	23	157	17,985	2635	2452	60	3189	2596	869	551	12,352

[a] SLO-266, -267, -175, -179, -1305, -165, -799, -497, -, -7, -8, -10 (Gobalet and Jones 1995) includes 1 salema, 1 brown Irish lord, 2 opaleye, 1 spotfin surfperch, 3 crisscross prickleback, 116 wolf eels, 2 *Citharichthys* sp., 1 arrowtooth flounder, 1 Dover sole, 1 C-O sole, 1 spotted cusk eel, 2 kelp perch, 29 gobies, 90 rainbow seaperch, 12 *Phanerodon* sp., 1 spotted turbot, 7 diamond turbot.

[b] includes 1 woolly sculpin.

[c] includes 1 penpoint gunnel, 1 salmon shark.

[d] includes 1 rockfish from SLO-1797.

[e] includes 1 rainbow surfperch, 19 gobies, and 3 wrasses.

[f] includes 1 salmon shark.

[g] Huddleston and Barker (1978) and Johnson (unpublished data) rockfishes include 1 kelp rockfish, 1 splitnose rockfish, 1 chilipepper, 2 vermilion rockfish, 7 swordfish, 1 sevengill shark, 1 common thresher shark, 4 diamond stingray.

[h] SBA-27, -48, -1900 (R. Salls unpublished data) rockfishes include 4 gopher rockfish, 1 treefish, 2 brown rockfish, 5 grass rockfish, 9 bocaccio, 2 specklefin midshipman, 18 albacore, 22 sevengill shark, 1 diamond turbot, 27 spotted turbot.

[i] SBA-71, -72, -73, -1674, -1731 (J. Johnson unpublished data).

[j] SBA-1807, -2057, -2061, Erlandson (1994).

Obispo County sites, is a strong reflection of their current zoogeographic range. This finding, however, must be qualified because the vertebrae of true smelts are so tiny that 1/16" mesh screens must be used in their recovery, and many collections lack or have limited materials of true smelts among their comparative materials (e.g. Zooarchaeology Laboratory, UCLA; faunal collection of the Department of Anthropology, UCSB; and Santa Barbara Museum of Natural History). Because of their tiny size, these fishes are likely to be missed during screening or during the subsequent faunal identification. Northern clingfish are an exclusively northern California species and are found only in northern sites. The identification of a single vertebra of *Paralabrax* at SLO-165 by Salls et al. (1989, in Gobalet and Jones 1995), and confirmed by this author by examination of the same sample, is the only element of the generally southern California genus found at San Luis Obispo County sites. This contrasts with 39 elements within the genus found to the south. Since only two Pacific barracuda have been found at San Luis Obispo County sites in contrast with 91 at the Santa Barbara County localities, the findings are consistent with expectations. In addition, Pacific barracuda elements are present in small numbers among midden materials on the Monterey, San Mateo, and Sonoma County coasts (Gobalet and Jones 1995, Gobalet 1997).

California sheephead remains are consistently found in southern California. None have been identified at the San Luis Obispo County sites, while at least four different investigators have found their remains in the southern area where they are currently more abundant. The few California sheephead remains found in Monterey County reported in Gobalet and Jones (1995) have not been verified by a second specialist.

The numerous monkeyface and rock prickleback elements found (including those identified only to family) exclusively at San Luis Obispo County (and even more abundant in middens in coastal Humboldt County sites in far northern California [Gobalet 1997]) strongly reinforce the hypothesis of zoogeographic range stability. Though found only among midden materials in the northern sites, crevice kelpfish are a more tentative indicator because three members of the genus *Gibbsonia* range far south of Pt. Conception. Only skeletal materials of *G. montereyensis* (crevice kelpfish) were available for comparative study. The few starry flounder found at San Luis Obispo County localities contrast with their extraordinary abundance at MNT-234 on Monterey Bay (Gobalet and Jones 1995) well to the north. Though they range to Santa Barbara (Eschmeyer et al. 1983), starry flounder would be rare at the extremes of their range and their scarcity or absence from the Santa Barbara County sites is expected.

Findings by Salls et al. (1989, in Gobalet and Jones 1995) of single elements of sargo, salema, two elements of opaleye, and seven elements of blacksmith at SLO-165 would, at first appearance, be findings inconsistent with their predicted occurrence. These identifications have not been confirmed through the examination of considerable additional material recovered during subsequent excavations of SLO-165. Four independent fish faunal specialists have been unable to confirm the presence of scales of northern anchovy, Pacific sardine, or bones of three genera of silversides, four genera of surfperches, California halibut, or opaleye in a sample of the materials evaluated by Salls et al. (1989, in Gobalet and Jones 1995) (Gobalet unpublished data). Consequently there is considerable suspicion that sargo, salema, blacksmith, and other elements have been misidentified as well.

Table 3. Species found generally only at archaeological sites in Santa Barbara County or San Luis Obispo County.

Santa Barbara County Sites	San Luis Obispo County Sites
horn shark	night smelt
shortfin mako	northern clingfish
swell shark	monkeyface prickleback
Paralabrax sp.	rock prickleback
California scorpionfish	crevice kelpfish
California sheephead	starry flounder
Pacific barracuda	Pacific tomcod
giant seabass	kelp greenling
rock wrasse	
queenfish	
white seabass	
sargo	
blacksmith	
California corbina	
yellowfin croaker	
black croaker	

The four sargo and 25 blacksmith remains Salls reported at sites in Santa Barbara County (Table 2) are within their expected range and would provide evidence to support the hypothesis, but they too require secondary verification. Additionally, secondary confirmation is required for two Pacific tomcod elements found only at SLO-165 and the finding of California scorpionfish, giant seabass, and rock wrasse remains only at Santa Barbara County sites.

Salls reported a stunning array of members of the drum family at three Santa Barbara County localities (Table 2): 10 California corbina, 10 yellowfin croaker, 265 white croaker, 13 queenfish, 3 black croaker, and 12 white seabass. Of these only white seabass have been reported in an independent study at SBA-1 by Huddleston and Barker (1978). Queenfish and white croaker, have been confirmed by other investigators from Santa Barbara County sites (Huddleston and Barker 1978, Erlandson 1994, Johnson unpublished data, Table 2). The large number of queenfish at Santa Barbara sites with 292 elements contrasting with only eight at the San Luis Obispo sites is consistent with their abundance within their present range. The drums reported by Salls would be expected at the southern sites, providing additional evidence for past and present zoogeographic consistency.

The presence of 16 confirmed or tentatively confirmed species mostly within their southern ranges and eight species with generally northern ranges collectively provide evidence that the prehistoric distribution of marine fishes to the immediate north or south of Pt. Conception has not changed from the time of Native American habitation to the present (Table 3). Contradictory data are few. Gray smoothhound, though rare north of Pt. Conception (Eschmeyer et al. 1983), were reported by Fitch (1972) at SLO-2 and confirmed at SLO-165 (Table 2). Their rarity, however, is consistent with their scarcity north of Pt. Conception (four elements at San Luis Obispo County sites versus 23 at Santa Barbara County sites). No soupfin shark have been found at the San Luis Obispo County sites, while being rather common at the Santa Barbara County localities. Soupfin shark range from British Columbia to Baja California (Eschmeyer et al. 1983). Pacific hake are typical finds in archaeological sites in central California (Gobalet and Jones 1995), but would be expected at the Santa Barbara County sites as well: they are absent. Though occasionally common off central California (Love 1996), Pacific bonito are lacking in the San Luis Obispo sites. The real surprise is that, given the vagaries of the archaeological record, there are not more species with unpredictable occurrence. The findings reported here are remarkably consistent with expectations.

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Age and Size of *Acacia* and *Cercidium* Influencing the Infection Success of Parasitic and Autoparasitic *Phoradendron*

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Abstract.—The degree of parasitic and autoparasitic *Phoradendron californicum* (desert mistletoe) infections on various ages and sizes of *Acacia gregii* (catclaw) and *Cercidium floridum* (blue palo verde) host trees was quantitatively investigated in southern Nevada and southeastern California. *Phoradendron californicum* commonly parasitized *A. greggii*, but occasionally parasitized *C. floridum* trees. Autoparasitic *P. californicum* infested another parasitic *P. californicum*, which, in turn, infested these two host species. Parasitism and autoparasitism of *P. californicum* were significantly positively correlated with age, and were consistently more correlated with size (height and canopy area) of *A. greggii* and *C. floridum*. Between the two host species, parasitism and autoparasitism were more positively correlated with age and size of *A. greggii*. Host age was significantly positively correlated with host size in both species. Area of parasite canopies was significantly greater than area of autoparasite canopies. A combination of age and size of *A. greggii* and *C. floridum* hosts partially limited the infection success of parasitic and autoparasitic *P. californicum* in southern Nevada and southeastern California.

Phoradendron species (mistletoes) are autotrophic obligate parasites inhabiting branches of higher vascular plants (Kuijt 1969; Calder and Bernardt 1983). Branches of their host plants often swell from overinfestation by *Phoradendron* species (Holland et al. 1977). *Phoradendron* species are green and leafy. They mainly derive water and various mineral nutrients from their host plants by direct xylem connections (Leonard and Hull 1965; Raven 1983; Kaufman 1989). Yet, the genus *Phoradendron* produces some of its food photosynthetically, and derives little or no carbohydrate from its hosts (Barbour et al. 1987). *Phoradendron californicum* (desert mistletoe) is a native parasitic plant that is sparsely distributed in southern Nevada and southeastern California. *Phoradendron californicum* frequently parasitizes several species of riparian and leguminous plant hosts, including *Prosopis glandulosa* (honey mesquite) and *Acacia greggii* (catclaw), but only occasionally parasitizes *Cercidium floridum* (blue palo verde), *Larrea tridentata* (creosote bush), and *Tamarix ramosissima* (saltcedar) trees (Holland et al. 1977).

The biology of *P. californicum* is well documented, indicating that this parasite physically taps host xylems to acquire water and various mineral nutrients from xylem fluids (Kuijt 1969; Walters 1976; Calder and Bernardt 1983; Ehleringer and Schulze 1985; Ehleringer et al. 1985 and 1986; Overton 1992; Jordan et al. 1997). *Phoradendron californicum* can also be epiparasitized by other *P. califor-*

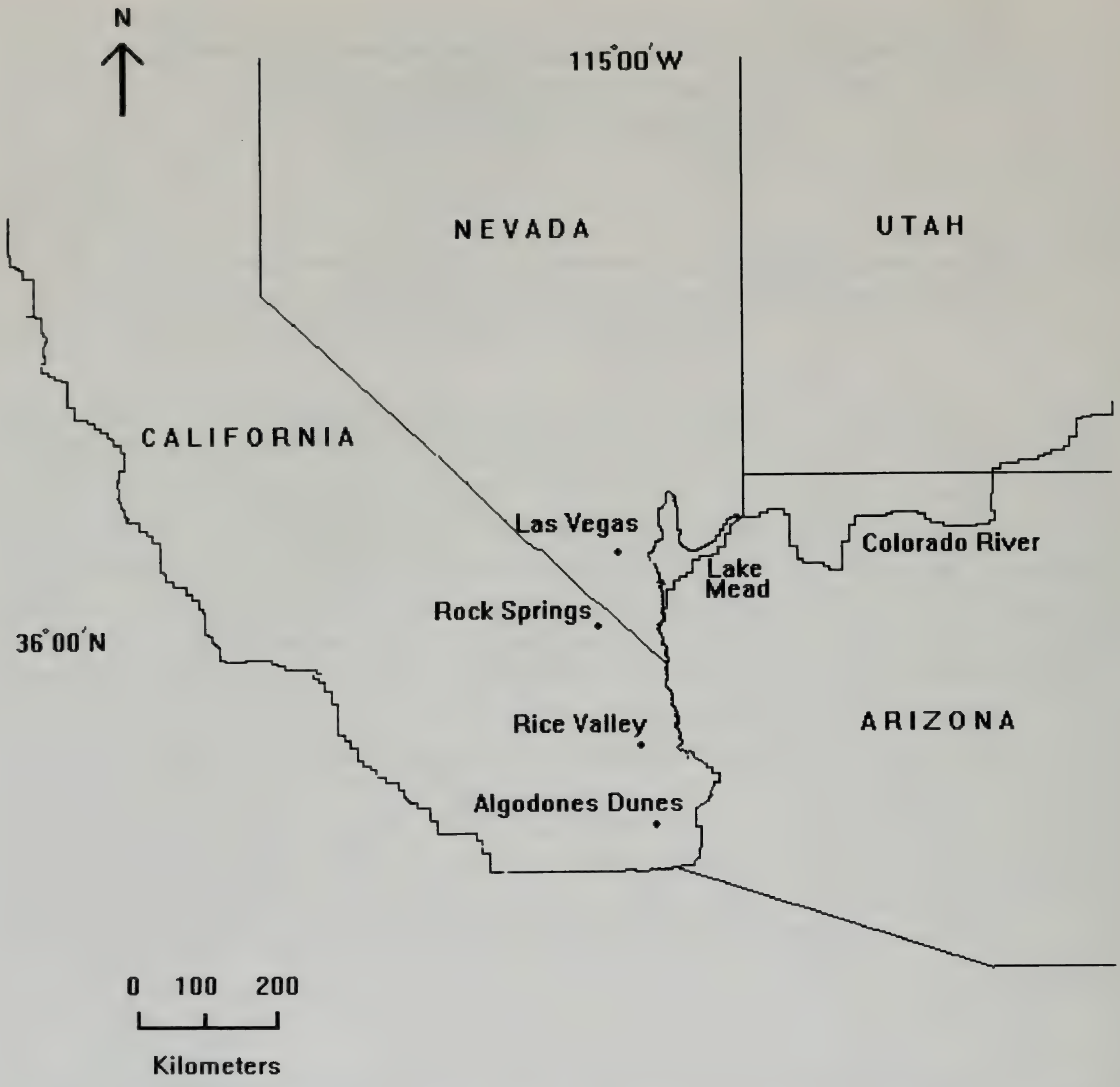
N
115°00'W
NEVADA
UTAH
CALIFORNIA
Las Vegas
Lake Mead
Colorado River
Rock Springs
36°00'N
ARIZONA
Rice Valley
Algodones Dunes
0 100 200
Kilometers

Fig. 1. Sketch map showing location of four *P. californicum* infection study sites in southern Nevada and southeastern California.

nicum individuals, which are in turn parasitic on *A. greggii* (Schulze and Ehleringer 1984) and *C. floridum* (blue palo verde) hosts (Ehleringer and Schulze 1985). This epiparasitic phenomenon, known as autoparasitism, occurs infrequently (Ehleringer and Schulze 1985). However, atypical host-parasite-autoparasite interactions involving the same three species remain poorly understood. This article examines to what degree age and size of *A. greggii* and *C. floridum* hosts affect the infection success of parasitic and autoparasitic *P. californicum* in southern Nevada and southeastern California.

Materials and Methods

Study Area and Field Measurements

Field studies were conducted in the Mojave and Colorado Deserts of southern Nevada and southeastern California, respectively, during the Fall of 1998 (Fig. 1). The Colorado Desert, ranging geographically from southeastern California to southwestern Arizona, is a major subdivision of the Sonoran Desert. *Phoraden-*

Table 1. Geographic characteristics of four *P. californicum* infection study sites in southern Nevada and southeastern California. Location, type of desert, as well as approximate elevation (m), latitude (N), and longitude (W) of these sites are shown. Study sites are arranged alphabetically within the Mojave Desert and Colorado Desert, a subdivision of the Sonoran Desert.

Study site	County, State	Latitude	Longitude	Elevation	Desert
Las Vegas Valley	Clark, NV	36°10′	115°05′	780	Mojave
Rock Springs	San Bernadino, CA	35°05′	115°00′	620	Colorado
Algodones Dunes	Imperial, CA	33°00′	115°10′	90	Colorado
Rice Valley	Riverside, CA	34°00′	114°50′	210	Colorado

dron californicum and its *A. greggii* hosts occur along dry wash habitats in southern Nevada and southeastern California, whereas *P. californicum* and its *C. floridum* hosts occur in low-elevation sandy habitats of southeastern California (Fig. 1 and Table 1). Various stages of *P. californicum* infections (light, moderate, and heavy) on *A. greggii* and *C. floridum* hosts were evident. From a distance, large clumps of *P. californicum* individuals, with or without autoparasites, are easily visible among the bare and nearly bare branches of their hosts, appearing as slightly lighter green or brownish-green patches on host plants.

Host species included individuals with parasitic and autoparasitic *P. californicum* (infested hosts) and included adjacent individuals without any visible *P. californicum* (control) on the canopies and branches. In Rock Springs and Las Vegas Valley, a total of 21 individuals of *P. californicum* were recorded as autoparasitic on other *P. californicum*, which were parasitic on nine *A. greggii* host trees. In Rice Valley and Algodones Dunes, a total of ten individuals of autoparasitic *P. californicum* were found growing indirectly on six *C. floridum* host trees. For this reason, 27 *A. greggii* and 18 *C. floridum* trees were evenly distributed among the three categories: hosts containing both parasites and autoparasites, hosts containing parasites only, and hosts without parasites at all. Uninfested hosts and hosts containing parasites only were randomly selected to provide unbiased sampling.

An incremental borer was used to extract a core of main stems through pith to estimate age of *A. greggii* and *C. floridum* hosts. No attempt was made to account for missing or false rings. Since missing rings are common in desert woody plants, absolute ages are likely to be underestimates (Tonnesen and Ebersole 1997). Within each infested host, all individuals of *P. californicum* (parasitic and autoparasitic) were counted. Host branch diameter and above-ground host branch height at the central point of *P. phoradendron* attachment were measured. Height and stem growth rate (diameter per ring) for main stems of infested and uninfested host plants were measured. Area of host, as well as area of parasitic and autoparasitic plant canopies were computed using the formula for the area of an ellipse.

Statistical Analyses

One-way analysis of variance (ANOVA) was performed to detect differences in age and size (height and canopy area) of infected and uninfected hosts. Tukey's Multiple Comparison Test (Analytical Software 1994) was used to compare means of host age, size, and stem growth rate when a significant infection effect was detected. Student's *t* test (Analytical Software 1994) was conducted to compare

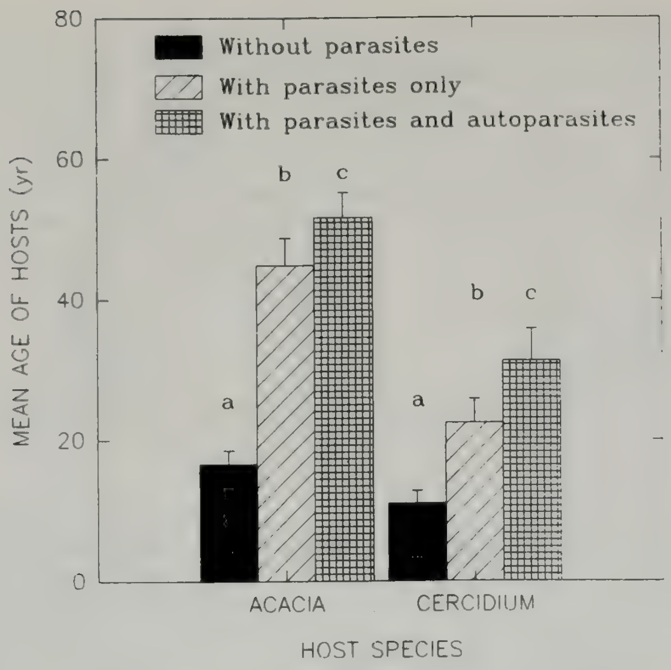

Fig. 2. Mean (± SE) age of *A. greggii* and *C. floridum* hosts with both parasites and autoparasites, with parasites only, and without any visible parasites (control) ($n = 27$ in *A. greggii* and $n = 18$ in *C. floridum* trees). Within the same host species, different letters at the top of columns indicate statistical significant at $P \leq 0.05$.

means of host branch diameter and above-ground host branch height, as well as to compare means of parasitic and autoparasitic canopy area in two host species. Pearsons correlation analysis (Analytical Software 1994) was performed to correlate abundance of *P. californicum* infection (total number of individuals on host canopy) with age and size of the two host species, and to autocorrelate the age and size of each host species. Mean values are presented with standard errors, and statistical significance is determined at $P \leq 0.05$.

Results

A number of *A. greggii* host trees were either uninfested or heavily infested by *P. californicum* plants (> 30 individuals per tree) in southern Nevada and southeastern California. Substantially more *A. greggii* trees were infested by *P. californicum* than *C. floridum* trees. Three hundred seventy-one (371) and 69 individuals of *P. californicum* were found parasitizing *A. greggii* and *C. floridum* trees, respectively. Age of the *Acacia greggii* stand was considerably older than age of the *C. floridum* stand (Fig. 2). *Acacia greggii* and *C. floridum* trees with *P. californicum* infestation were significantly ($P \leq 0.001$) older (Fig. 2), taller (Fig. 3), and larger (Fig. 4) compared to adjacent uninfected hosts of the same species. *Acacia greggii* and *C. floridum* hosts showing autoparasitism were significantly ($P \leq 0.001$) older, taller, and larger than hosts showing moderate parasitism (Figs. 2–4). Older, taller plants had a significantly greater stem diameter than younger, shorter plants (data not shown). However, stem growth rates (mean width of annual growth rings) for main stems of parasitized and unparasitized trees in both species were not significantly different ($P > 0.05$; Table 2). Individuals of *P. californicum* primarily inhabited hosts' secondary branches, although some individuals were found at the junction of main trunks and secondary branches.

High levels of *P. californicum* infestation were significantly positively correlated ($P \leq 0.001$; Table 3) with age and size of *A. greggii* and *C. floridum* hosts.

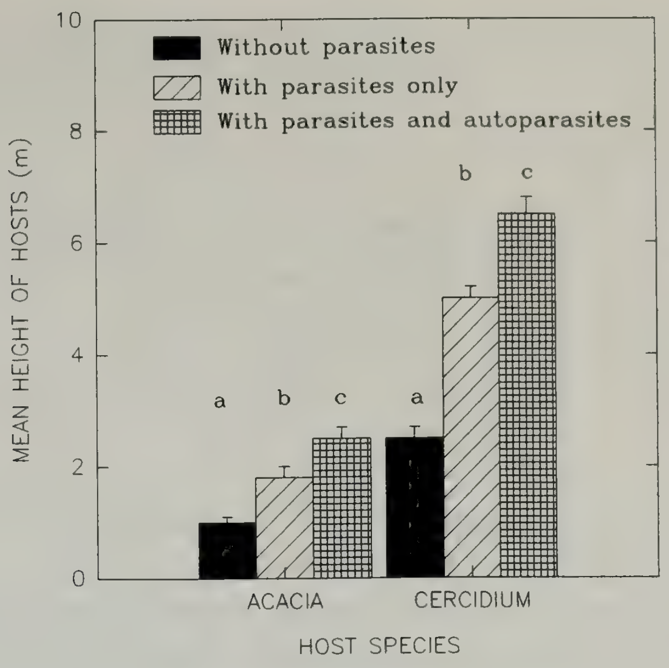

Fig. 3. Mean (± SE) height of *A. greggii* and *C. floridum* hosts with both parasites and autoparasites, with parasites only, and without any visible parasites (control) (n = 27 in *A. greggii* and n = 18 in *C. floridum* trees). Within the same host species, different letters at the top of columns indicate statistical significant at $P \leq 0.05$.

In both cases, parasitism and autoparasitism were most positively correlated with host canopy area, while least positively correlated with host age. Between the two host species, the abundance of *P. californicum* was more positively correlated (Table 3) with age, height, and canopy area of *A. greggii*.

All possible two-way interactions between the age and size (height and canopy area) of *A. greggii*, as well as between the age and size of *C. floridum* hosts revealed significant positive correlations ($P \leq 0.001$; Table 4). The greatest positive correlation was consistently found between height and canopy area in both host species ($P \leq 0.001$; Table 4).

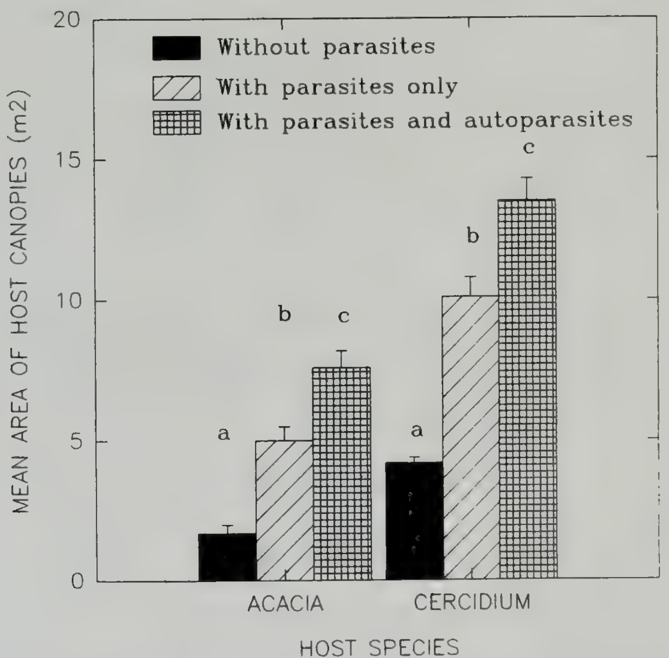

Fig. 4. Mean (± SE) area of *A. greggii* and *C. floridum* host canopies with both parasites and autoparasites, with parasites only, and without any visible parasites (control) (n = 27 in *A. greggii* and n = 18 in *C. floridum* trees). Within the same host species, different letters at the top of columns indicate statistical significant at $P \leq 0.05$.

Table 2. Mean (± *SE*) stem growth rates (diameter per ring) of *A. greggii* and *C. floridum* hosts with both parasites and autoparasites, with parasites only, and without any visible parasites (control) ($n = 9$ in *A. greggii* and $n = 6$ in *C. floridum* trees). Mean values in rows followed by the same letter are not significantly different ($P > 0.05$).

Host species	Mean Width of Annual Rings (cm/ring count)		
	Control	Parasites only	Autoparasites
A. greggii	0.51 ± 0.04 a	0.54 ± 0.04 a	0.56 ± 0.03 a
C. floridum	0.57 ± 0.03 a	0.60 ± 0.04 a	0.62 ± 0.04 a

Mean heights and stem diameters of *P. californicum*-infested host branches, with or without autoparasites, did not differ significantly ($P > 0.05$; Table 5) in both *A. greggii* and *C. floridum* trees. Since *C. floridum* were considerably taller than *A. greggii* trees, *P. californicum* often established at *C. floridum* branches with a greater vertical distance from the ground surface. Areas of parasitic *P. californicum* canopies were significantly ($P \leq 0.05$; Table 5) greater than areas of autoparasitic canopies. Areas of parasite and autoparasite canopies were substantially greater in *A. greggii* than in *C. floridum* trees (Fig. 5), even though *C. floridum* hosts were taller and had a considerably greater canopy area (Figs. 3–4).

Discussion

The degree of parasitic and autoparasitic *P. californicum* infestation on various ages and sizes of *A. greggii* and *C. floridum* hosts was examined in southern Nevada and southeastern California. Within each host species, data from two study sites were pooled to detect the significance of host age and size factors that appear to play a vital role in limiting *P. californicum* infection success. Ehleringer and Schulze (1985) saw occasional individuals of *P. californicum* parasitized others of the same species, which, in turn, grew on their *A. greggii* and *C. floridum* hosts near Oatman, Arizona. Nevertheless, no data from previous investigations are available to compare correlations between the abundance of parasitic and autoparasitic *P. californicum* and the age and size of their host plants species.

There are several potential explanations for the higher levels of *P. californicum* infestation exhibiting a clumped distribution in older, taller, and larger *A. greggii* and *C. floridum* hosts. First, many taller, larger trees were significantly older with

Table 3. Correlations (*r*-value) between the abundance of *P. californicum* and the age and size (height and canopy area) of *A. greggii* and *C. floridum* hosts (371 individuals of *P. californicum* growing on 27 *A. greggii* and 69 individuals growing on 18 *C. floridum* trees). Significance levels: *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$; NS: Non-significant.

Host species	Interaction	*r*-value
A. greggii	Host age × *P. californicum* abundance	0.80***
	Host height × *P. californicum* abundance	0.84***
	Host canopy area × *P. californicum* abundance	0.86***
C. floridum	Host age × *P. californicum* abundance	0.68**
	Host height × *P. californicum* abundance	0.73***
	Host canopy area × *P. californicum* abundance	0.81***

Table 4. Correlations (r-value) between the age and size (height and canopy area) of *A. greggii* and *C. floridum* hosts. Significance levels: *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$; NS: Non-significant.

Host species	n	Interaction	r-value
A. greggii	27	Age × height	0.82***
		Age × canopy area	0.84***
		Height × canopy area	0.88***
C. floridum	18	Age × height	0.77***
		Age × canopy area	0.82***
		Height × canopy area	0.86***

a significantly greater stem diameter than shorter, smaller trees. This phenomenon may indicate a time dependent *P. californicum* colonization rate (Lei 1999). In this study, autoparasitic *P. californicum*-infested hosts were significantly older than parasitic *P. californicum*-infested hosts, which were significantly older than uninfested hosts. Through time, *P. californicum* infestation intensifies considerably; the longer a host tree lives, the more opportunities for successful autoparasites infestation. In this study, the abundance of parasites and autoparasites increased significantly with increasing host age irrespective to host stem growth rate. Second, large host tree size would provide a greater surface area, indicating more widespread secondary branches available for successful *P. californicum* colonization and establishment (Lei 1999). In this study, most *A. greggii* trees exhibited multiple trunks, whereas *C. floridum* trees exhibited either single or multiple trunks in relatively even frequencies. Mature or long-lived host trees were significantly taller and had a significantly greater canopy size compared to juvenile or short-lived trees of the same species in this study. Increasing in tree size, along with a greater surface area, may increase the host susceptibility of extensive *P. californicum* colonization and infestation, as evidenced by autoparasites inhabiting some of the tallest and largest hosts. Third, seeds of *P. californicum* are often dispersed by birds as they feed. Birds, such as *Phainopepla nitens* (phainopepla) and *Minus polyglottos* (northern mockingbird), ingest the seeds and may remain long enough on the infested hosts to deposit or defecate them onto branches of the same host plant (Haigh 1996). Fourth, dispersal of *Phoradendron* seeds can also be influenced by arboreal mammals and by gravity, but these are likely to be rare and minor mechanisms (Calder and Bernhardt 1983). Fifth, seeds of *Phoradendron* species can be ejected from the fruits without avian or animal assistance (Kuijt 1969). These seeds may land on the same host plant through maternal

Table 5. Mean (± *SE*) host branch diameters and branch heights at the central points of parasitic and autoparasitic *P. californicum* attachments on *A. greggii* ($n = 9$) and *C. floridum* ($n = 6$) hosts. Mean values in rows followed by the same letter are not significantly different ($P > 0.05$).

Host species	Host branch diameter (cm)		Host branch height (m)	
	Parasite	Autoparasite	Parasite	Autoparasite
A. greggii	2.7 ± 0.2 a	3.0 ± 0.3 a	1.0 ± 0.1 a	0.7 ± 0.1 a
C. floridum	2.9 ± 0.2 a	3.2 ± 0.2 a	2.5 ± 0.2 a	2.1 ± 0.2 a

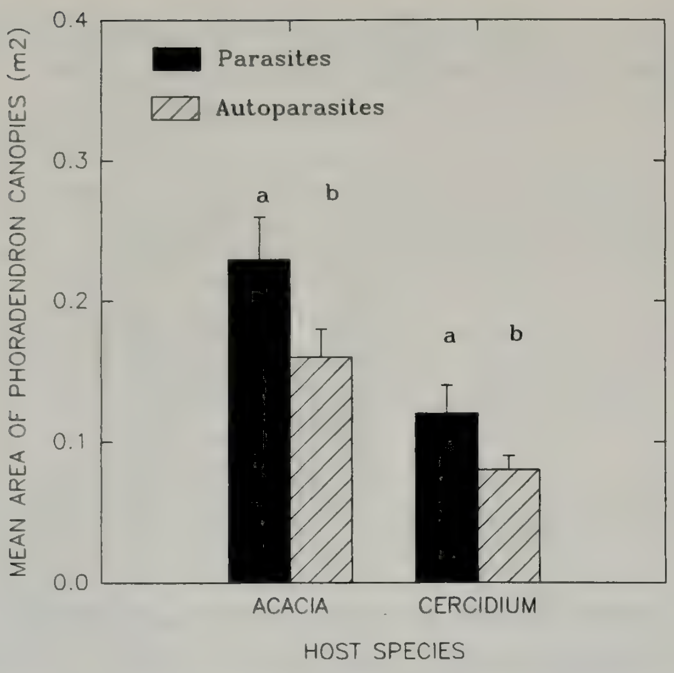

Fig. 5. Mean (± SE) area of parasitic and autoparasitic *P. californicum* canopies (371 individuals of *P. californicum* growing on 27 *A. greggii* and 69 individuals growing on 18 *C. floridum* host trees). Within the same host species, different letters at the top of columns indicate statistical significant at $P \leq 0.05$.

influence or may land on another host, stick to its branches and germinate there (Belzer 1984).

Although not examined in this study, significantly older, taller, and larger hosts may contain higher moisture content and nutritional value relative to younger, shorter, and smaller trees. In general, a number of essential nutrients, including N, P, K, Ca, Mg, and Fe, are found highest in the autoparasitic *P. californicum* and lowest in the *A. greggii* hosts in northwestern Arizona (Ehleringer and Schulze 1985). In an parasite-autoparasite system involving *P. californicum* with *A. greggii* as the host, water use efficiency is highest in the host and lowest in the autoparasite, while transpiration rate appears to be greatest in the autoparasite and lowest in the host in northwestern Arizona (Schulze and Ehleringer 1984; Ehleringer and Schulze 1985). The concepts of water use efficiency, as well as water and mineral nutrient acquisition from their hosts may partially explain a smaller canopy size observed in autoparasites than in parasites because a large canopy is energetically expensive to maintain over a long period of time. From casual observations, autoparsites had little or no direct contact with host branches and xylems. Parasites obtain limited water and nutrients from their hosts; autoparasites, in turn, obtain even more limited resources from their parasitic hosts. Low host-plant water potentials and water content may limit long-term *P. californicum* infection success in southern California (Jordan et al. 1997). Small, young trees may not have the physiological capabilities (insufficient water supply and essential nutrients) to support long-term parasitic and autoparasitic *P. californicum* infection and reproductive success. Since both parasitic and autoparasitic *P. californicum* tap to the same *A. greggii* host xylems (Ehleringer and Schulze 1985), they must constantly acquire limited resources from, and at the expense of, their *A. greggii* and *C. floridum* hosts.

The distribution of *Phoradendron californicum* is scanty, and *P. californicum* is not an extremely important component of the Mojave and Colorado desert vegetation in southern Nevada and southeastern California, respectively. Yet, localized influences of *P. californicum* on *A. greggii* and *C. froidum* hosts are conspicuous. Host age and size were two of the main factors that limited the long-term infection success of *P. californicum*. Larger, taller *A. greggii* and *C. floridum* plants were significantly older, and were significantly more likely to be infested with the parasites than younger, small plants. Within the same host species, trees exhibiting autoparasitism were significantly older, taller, and larger than trees exhibiting moderate or no parasitism. However, relationships between the infection success of *P. californicum* and the age and size of *A. greggii* and *C. floridum* hosts were purely correlative. Correlation between two variables does not necessarily mean that a cause-effect relationship actually exists between them. Host age and size appear to be strongly related to the availability of water and mineral nutrients. Future research at various geographical locations are required to determine cause-effect relationships between the long-term infection or reproductive success of parasitic and autoparasitic *P. californicum* and the age, size, water and nutrient status of their host species.

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Research Note

Helminths of the Channel Islands Slender Salamander, *Batrachoseps pacificus pacificus* (Caudata: Plethodontidae) from California

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The Channel Islands slender salamander, *Batrachoseps p. pacificus* (Cope 1865) is restricted to San Miguel, Santa Rosa, Santa Cruz and Anacapa Islands off the coast of Santa Barbara, California (Petranka 1998). The blackbelly slender salamander, *B. nigriventris* Cope 1869 occurs in sympatry with *B. p. pacificus* on Santa Cruz Island (Petranka 1998). The Pacific treefrog, *Hyla regilla* Baird and Girard 1852, western fence lizard, *Sceloporus occidentalis* Baird and Girard 1852, side-blotched lizard, *Uta stansburiana* Baird and Girard 1852, southern alligator lizard, *Elgaria multicarinata* (Blainville 1835), eastern racer, *Coluber constrictor* Linnaeus 1758, gopher snake, *Pituophis catenifer* (Blainville 1835) and spotted night snake, *Hypsiglena torquata ochrorhyncha* Cope 1860 also occur on Santa Cruz Island (Savage 1967). Populations of these species on Santa Cruz Island have not been examined for helminths; however, adjacent mainland populations (Los Angeles County, CA), of *B. nigriventris, H. regilla, S. occidentalis*, and *U. stansburiana* have been studied (Koller and Gaudin 1977; Goldberg et al. 1998a, 1998b, 1999). The purpose of this study was to determine the helminth fauna of a population of the channel islands slender salamander, *B. p. pacificus*.

One hundred seventy four *B. p. pacificus* were examined: 96 females, mean snout-vent length (SVL) = 40.5 mm ± 7.1 SD, range 27–56 mm; 78 males, SVL = 40.2 mm ± 6.6 SD, range 28–54 mm were examined. There was no significant difference in SVL between male and female subsamples (ANOVA, $F = 0.86$, $P > 0.05$). These salamanders were collected in the western portion of the central valley of Santa Cruz Island, Santa Barbara County, California (33°65′N, 119°42′W to 34°01′N, 119°52′W), elevation about 76 m, March 1971 and have been deposited in the herpetology collection of the Natural History Museum of Los Angeles County (LACM 144880–145053).

The body cavity was opened, the gastrointestinal tract removed and the esophagus, stomach, small intestine, large intestine, bladder and body cavity of each specimen was examined separately under a dissecting microscope. Each nematode was removed and placed in a drop of glycerol on a glass slide. Some cestode larvae were stained regressively with hematoxylin, others were embedded in paraffin, cut into 5 μm sections, mounted on glass slides and stained with hematoxylin followed by eosin counterstain. All specimens were examined with a compound microscope. Terminology is in accordance with Bush et al. (1997).

Ninety nine salamanders (57%) harbored helminths (Table 1): 50 females

Table 1. Prevalence, mean intensity and abundance of helminths from *Batrachoseps p. pacificus* from Santa Cruz Island, CA.

Helminth	Number helminths	Site of infection	Prevalence[1] %	Mean intensity ±SD	Range	Mean abundance[2] ±SD
Cestoda						
Mesocestoides sp. (tetrathyridia)	48	coelom	1	48	—	0.3 ± 3.6
Nematoda						
Batracholandros salamandrae	183	large intestine	54	1.9 ± 2.6	1–25	1.1 ± 2.2
Oswaldocruzia pipiens	27	small, large intestine	9	1.8 ± 1.7	1–7	0.2 ± 0.7

[1] Number of hosts infected with one or more individuals of a parasite species divided by the number of hosts examined.

[2] Total number of individuals of a parasite species divided by the total number of hosts examined.

(52%), 49 males (63%). There was no significant difference in prevalence between male and female salamanders, Chi square = 1.26, $P > 0.05$. One male salamander (54 mm) had 48 tetrathyridia of the cestode *Mesocestoides* sp. encysted on its liver. Ninety four salamanders (54%) 48 females, 46 males, harbored 183 individuals of the nematode *Batracholandros salamandrae* (Schad 1960), and 15 salamanders (9%), 6 females, 9 males harbored 27 individuals of the nematode *Oswaldocruzia pipiens* Walton 1929. There was no significant difference for prevalence between male and female salamanders, Chi square = 1.39, 1.52, respectively, $P > 0.05$. Likewise, there was no relationship between SVL and helminth intensity, $r^2 = 0.19$. Ten salamanders had dual infections of *B. salamandrae* and *O. pipiens*; 1 salamander had a dual infection of *Mesocestoides* sp. and *B. salamandrae*. Each helminth infection represents a new host and locality record. Representative helminths were placed in vials of alcohol and deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland: USNPC # 88523 *Mesocestoides* sp.; USNPC # 88524 *Batracholandros salamandrae*; USNPC # 88525 *Oswaldocruzia pipiens*.

Tetrathyridia of *Mesocestoides* sp. are commonly found in amphibians and reptiles (McAllister 1988; McAllister and Conn 1990); however, this is apparently the first report of *Mesocestoides* sp. from a salamander. *Batracholandros salamandrae* has previously been reported from salamanders of southern California as well as North America in general and is apparently restricted to the order Caudata (Goldberg et al. 1998a). *Oswaldocruzia pipiens* is a host generalist, occurring in amphibians and reptiles throughout North America (Baker 1987).

Helminth communities of salamanders are difficult to analyze due to low species richness and dominance of the community by host generalists. Aho (1990) found salamanders in general to have per host individual a mean species richness of 0.70 ± 0.04 SE and mean abundances of 5.2 ± 1.38 SE. Mean species richness of helminths per host for this population of *Batrachoseps p. pacificus* was 0.63 ± 0.05 SE and mean abundance of helminths was 1.40 ± 0.33 SE.

Apparently, the only other study of insular salamanders is that of Moravec (1984) in which the roughskin newt, *Taricha granulosa* (Skilton 1849) (N = 10) was found to harbor two species of Trematoda *Megalodiscus microphagus* Ingles 1936, *Brachycoelium salamandrae* (Froelich 1789), and three species of Nematoda, *Cosmocercoides variabilis* (Harwood 1930), *Hedruris siredonis* Baird 1858, *Megalobatrachonema gigantica* (Olsen 1938). Species richness and mean abundance cannot be calculated for the sample of *T. granulosa*. But, as was true of the helminths harbored by *B. p. pacificus*, the helminths harbored by *T. granulosa* are found in adjacent mainland amphibian hosts (Baker 1987). Insular populations appear to follow the prediction of Goldberg et al. (1998a) that salamander species have helminth communities characterized by low species richness and dominated by host generalists.

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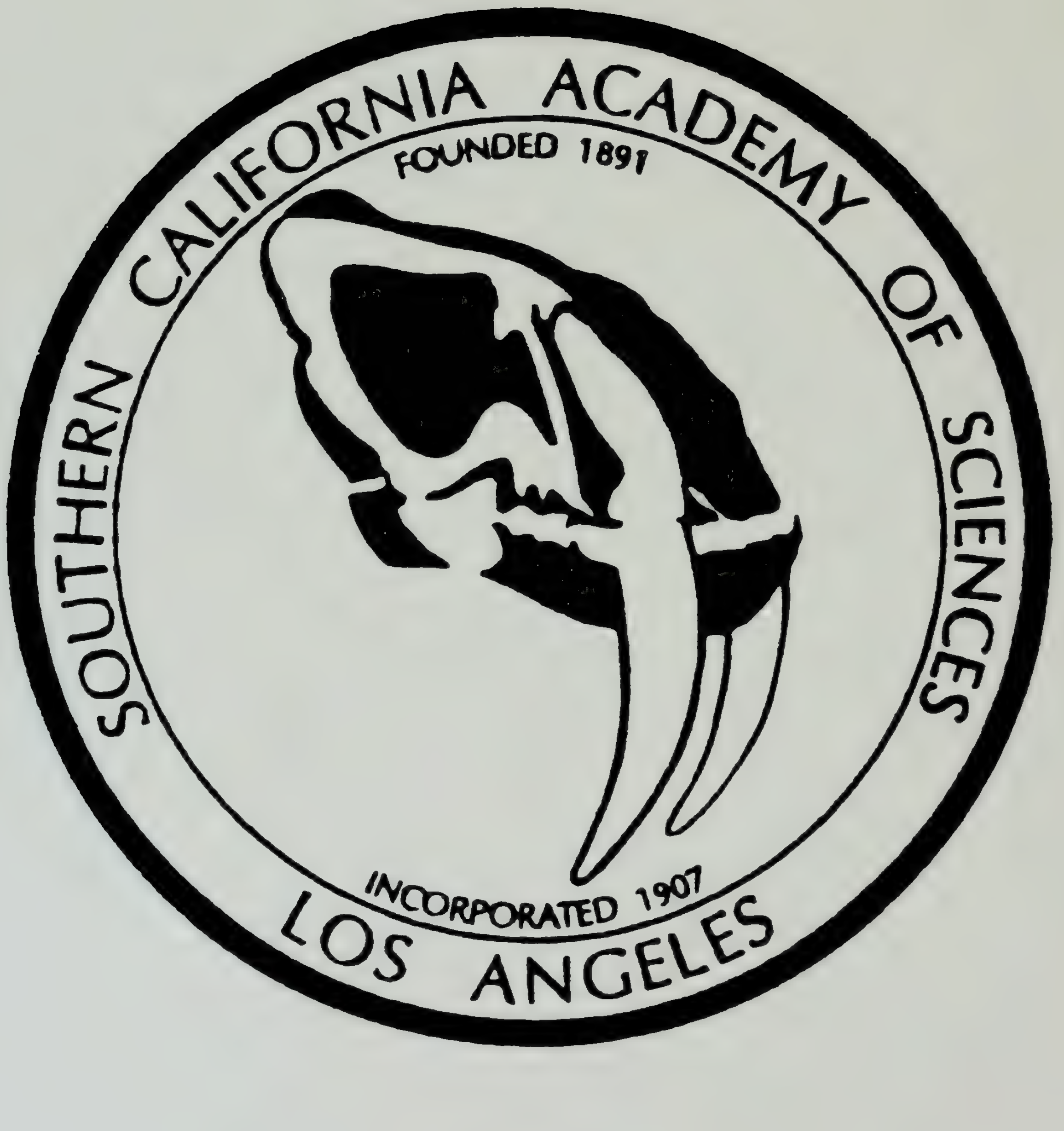
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Ecological and Distributional Status of the Continental Fishes of Northwestern Baja California, Mexico

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Abstract.—The ecological and distributional status of the continental fishes of northwestern Baja California, Mexico, was seasonally monitored between February 1996 and March 1997. A review of records in literature and of specimens collected between 1983 and 1995 in the study area, provide the data upon which this report is based. A total of 23 species (19 native and 4 exotic) belonging to 22 genera and 15 families was registered. This fish fauna is ecologically composed of species of marine derivation (78.9% sporadic and 21.1% diadromous) and by 8 permanent species (34.8%), 9 tidal visitors (39.1%) and 6 occasional visitors (26.1%). From the ichthyogeographical point of view, most of the species are of Californian affinity (68.4%) and the remaining related to northeastern Pacific (15.7%), Holarctic (5.3%) and circumtropical (5.3%) regions. Only one taxon (*Oncorhynchus mykiss nelsoni*) is endemic (5.3%) to the study region. Ten species are new continental records for Baja California [Norte], and seven taxa reach their southernmost continental ranges in northwestern Baja California. The conservation status of *Gasterosteus aculeatus microcephalus* is considered as threatened. The main problem that affects the ecosystemic integrity of the streams of this region is the progressive alteration of the aquatic and riparian habitats caused by anthropogenic impact.

Resumen.—El estatus ecológico y distributivo de los peces continentales del noroeste de Baja California, México, fue evaluado estacionalmente entre Febrero 1996 y Marzo 1997. Una revisión de registros de literatura y de ejemplares recolectados entre 1983 y 1995 en el área de estudio, complementan los datos que soportan el presente estudio. Un total de 23 especies (19 nativas y 4 exóticas) pertenecientes a 22 géneros y 15 familias fue registrado. La ictiofauna continental se compone ecológicamente por especies de estirpe marina (78.9% esporádicas y 21.1% diadromas) y en función de tiempo por 8 especies permanentes (34.8%), 9 visitantes de marea (39.1%) y 6 visitantes ocasionales (26.1%). Desde un punto de vista ictiogeográfico, la mayoría de las especies son de afinidad California (68.4%) y el resto a las regiones del océano Pacífico Nororiental (15.7%), Holártica (5.3%) y Circumtropical (5.3%). Solamente un taxón (*Oncorhynchus mykiss nelsoni*) es endémico (5.3%) al área de estudio. Diez especies representan nuevos registros en las aguas continentales de Baja California, y siete especies alcanzan sus distribuciones continentales más sureñas en el noroeste de Baja California. El estatus de conservación de *Gasterosteus aculeatus microcephalus* es considerado como amenazado. El principal factor que atenta la integridad ecosistémica de los arroyos de esta región es la alteración progresiva de los hábitats acuáticos y ribereños causada por impacto antropogénico.

The northwestern region of Baja California, Mexico, which includes the San Diego and San Pedro Mártir faunistic districts, is of special interest due to its ecological and biogeographical peculiarities (Nelson 1921; Bancroft 1926). Its native continental fish fauna is entirely dominated by species of marine derivation or peripheral (Follett 1960; Ruiz-Campos and Contreras-Balderas 1987).

The scarce representation of perennial streams in the Baja California peninsula (Blásquez 1959; Tamayo and West 1964; Murvosh 1994; INEGI 1995), combined with the paleohydrological discontinuity of its northwest region with that of southern California, as well as the great steepness of its eastern coast (Follett 1960) have been considered as the causative factors of the null dispersion of secondary and primary freshwater fishes (Myers 1951; Miller 1966) and the consequent invasion and establishment by fishes of marine derivation (e.g., vicarious, diadromous, sporadic and complementary; Follett 1960; Ruiz-Campos and Contreras-Balderas 1987).

Follett (1960) and Ruiz-Campos and Contreras-Balderas (1987) in their annotated check-lists of the continental fishes of the Baja California peninsula, cited only 13 species (6 native and 7 exotic) for the northwest region, the majority of which were from collections limited in time and space that were carried out about four decades ago.

From the ichthyogeographical point of view, several taxa exist that reach their southernmost continental distribution ranges in northwestern Baja California; *Lampetra tridentata* Gairdner (Ruiz-Campos and González-Guzmán 1996), *Fundulus parvipinnis parvipinnis* Girard (Miller 1943), *Gasterosteus aculeatus microcephalus* Girard (Miller and Hubbs 1969), and *Leptocottus armatus australis* Hubbs (Follett 1960). Additionally, one endemic taxon exists, the Nelson's trout, *Oncorhynchus mykiss nelsoni* (Evermann), which is confined to the streams of the western slope of the Sierra San Pedro Mártir (Ruiz-Campos 1993; Ruiz-Campos and Pister 1995).

In general terms, the continental ichthyofauna of the northwestern Baja California has been scarcely studied at ecological and taxonomical levels as compared with that of southern California (Swift et al. 1993). During the last two decades this region, particularly its coastal stripe, has been the focus of a growing anthropogenic activity (e.g., urban, tourist, industrial and agricultural development) that puts at risk the stability of its aquatic and riparian ecosystems.

The conservation of the aquatic ecosystems, especially those near the coast, is vital because they operate as reproduction and nursery habitats for a diversity of peripheral fishes, whose adult stages make up important links in the food chains of coastal environments or are of importance to fisheries (Horn and Allen, 1985; Horn, 1988; Zedler et al. 1992). Also, these biotopes are used by winter migrant birds that travel along the Pacific flyway (Ruiz-Campos and Rodríguez-Meraz 1993).

For that reason, the present study evaluates the ecological and distributional status of the fish fauna inhabiting the coastal streams of northwestern Baja California, Mexico. This study is mainly based on seasonal fish samplings carried out in twelve coastal streams during the period of 1996–1997. In addition, a review of literature records as well as specimens collected between 1983 and 1995, complete the data upon which this study is based. Finally, the information generated here can be used to support future conservation programs to protect regional biodiversity.

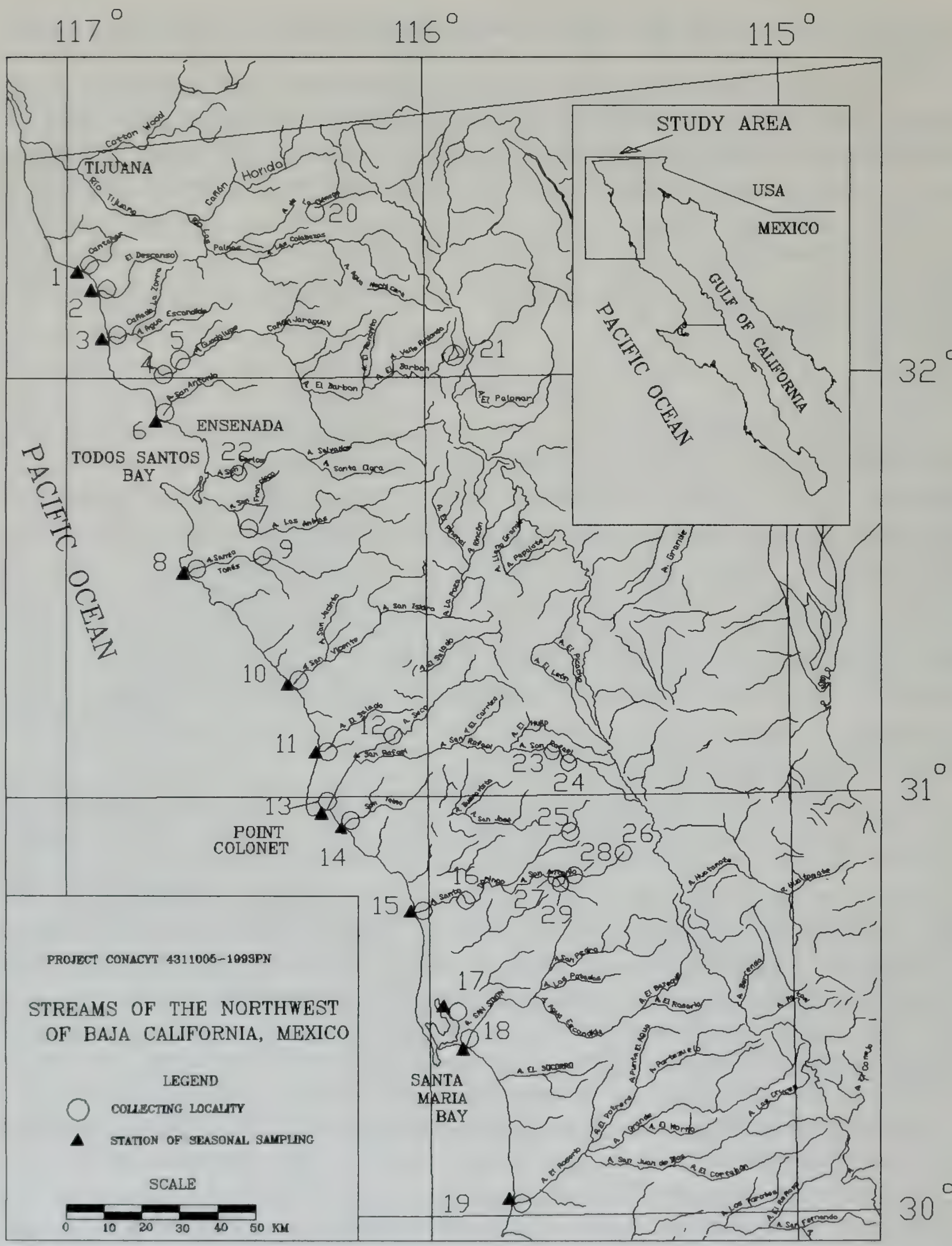
Study Area

The northwestern region of Baja California is characterized by possessing a mediterranean-type climate and exhibiting a distinctive pattern of rainy winters followed by dry summers (Archibold 1995). Its surface hydrology is represented by a series of small streams originating on the western slopes of the Sierras Juárez and San Pedro Mártir, which flow toward the Pacific Ocean (Fig. 1). Most of these streams (Figs. 2 and 3) become intermittent in their middle and lower courses during extremely dry conditions (Tamayo and West 1964). The mouths of most streams are blocked from the ocean by sandbars, except during extreme flooding events or high tides that produce riverine-estuarine conditions. However, some streams (e.g., Santo Tomás, El Salado, San Simón and El Rosario) are permanently open to the sea due to tidal inflows.

The average values of the physical-chemical variables registered seasonally in the studied streams are presented in Table 1. The salinity of the water was highly variable for most sampled streams and it was dependent of the opening or closing of the mouth during the big freshwater flows or the inflows of sea water at high tide. Localities at the mouths of the arroyos Cantamar, El Descanso, San Miguel (El Carmen) exhibited little variation in salinity during the year because their mouths were frequently closed by sandy bars that prevented the entry of the high tide flows (Table 1). Most of the streams studied registered average pH values of slightly alkaline (7 to 9) and few were moderately alkaline (9 to 10). These pH variations were dependent on the alternation of freshwater and high tide flows.

Other variables such as conductivity and total dissolved solids (TDS), exhibited seasonal variations in their average values at each locality studied.

The riparian vegetation associated to the upper and middle courses of the streams is represented by Arroyo Willow (*Salix lasiolepis*), Red Willow (*S. laevigata*), Fremont Cottonwood (*Populus fremontii*), Western Sycamore (*Platanus racemosa*) and Coast Live Oak (*Quercus agrifolia*) (Wiggins 1980). The lower parts of the streams possess brackish marsh vegetation including Cattail (*Typha domingensis*), Ditch Grass (*Ruppia maritima*), Spiny Rush (*Juncus acutus*), Annual Pickleweed (*Salicornia bigelovii*), Saltgrass (*Distichlis spicata*) and Bulrushes (*Scirpus californicus*) (Delgadillo-Rodríguez et al. 1992). Aquatic macrophytes found along the streams, include *Berula erecta, Ceratophyllum demersum, Chara* sp., *Potamogeton natans,* and *Ranunculus aquatilis* (Ruiz-Campos 1993; Ruiz-Campos and Pister 1995).


117°
116°
115°
32°
31°
30°
STUDY AREA
USA
MEXICO
GULF OF CALIFORNIA
PACIFIC OCEAN
Cotton Wood
TIJUANA
Río Tijuana
Cañón Hondo
Cantamar
El Descanso
ENSENADA
TODOS SANTOS BAY
PACIFIC OCEAN
POINT COLONET
SANTA MARIA BAY
El Barbon
El Palomar
A. San Antonio
A. Salvador
Santa Clara
A. Los Ambles
A. San Isidro
A. San Vicente
A. San Jacinto
A. El Salado
A. San Rafael
A. San Telmo
A. San José
A. Santo Domingo
A. San Simón
A. San Pedro
A. Los Pabellones
A. Agua Escondida
A. El Socorro
A. El Rosario
A. Grande
A. San Juan de Dios
A. El Carrizo
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PROJECT CONACYT 4311005-1993PN
STREAMS OF THE NORTHWEST OF BAJA CALIFORNIA, MEXICO
LEGEND
○ COLLECTING LOCALITY
▲ STATION OF SEASONAL SAMPLING
SCALE
0 10 20 30 40 50 KM

Fig. 1. Geographical situation of the study area and of the fish collecting localities in northwestern Baja California, México. Black triangles indicate localities monitored during an annual cycle (February 1996-March 1997). See appendix 1 for description of localities.

Methods

Fish samplings were carried out in different streams of the northwestern Baja California, México, between 1983 and 1997 (Fig. 1, Appendix 1). Twelve streams

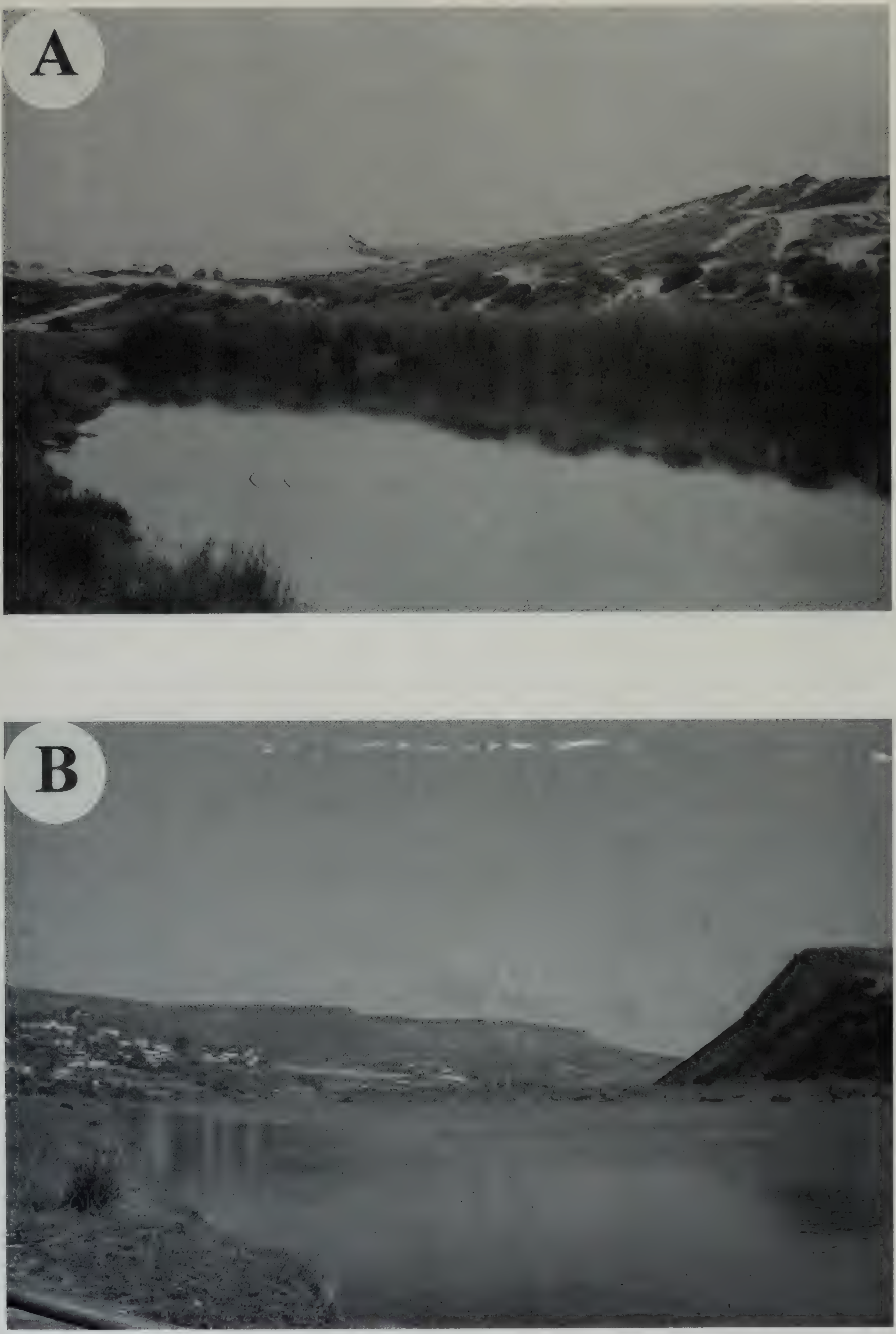

Fig. 2. (A) Slough adjacent to mouth of Arroyo El Descanso. (B) lower part of Arroyo La Misión.

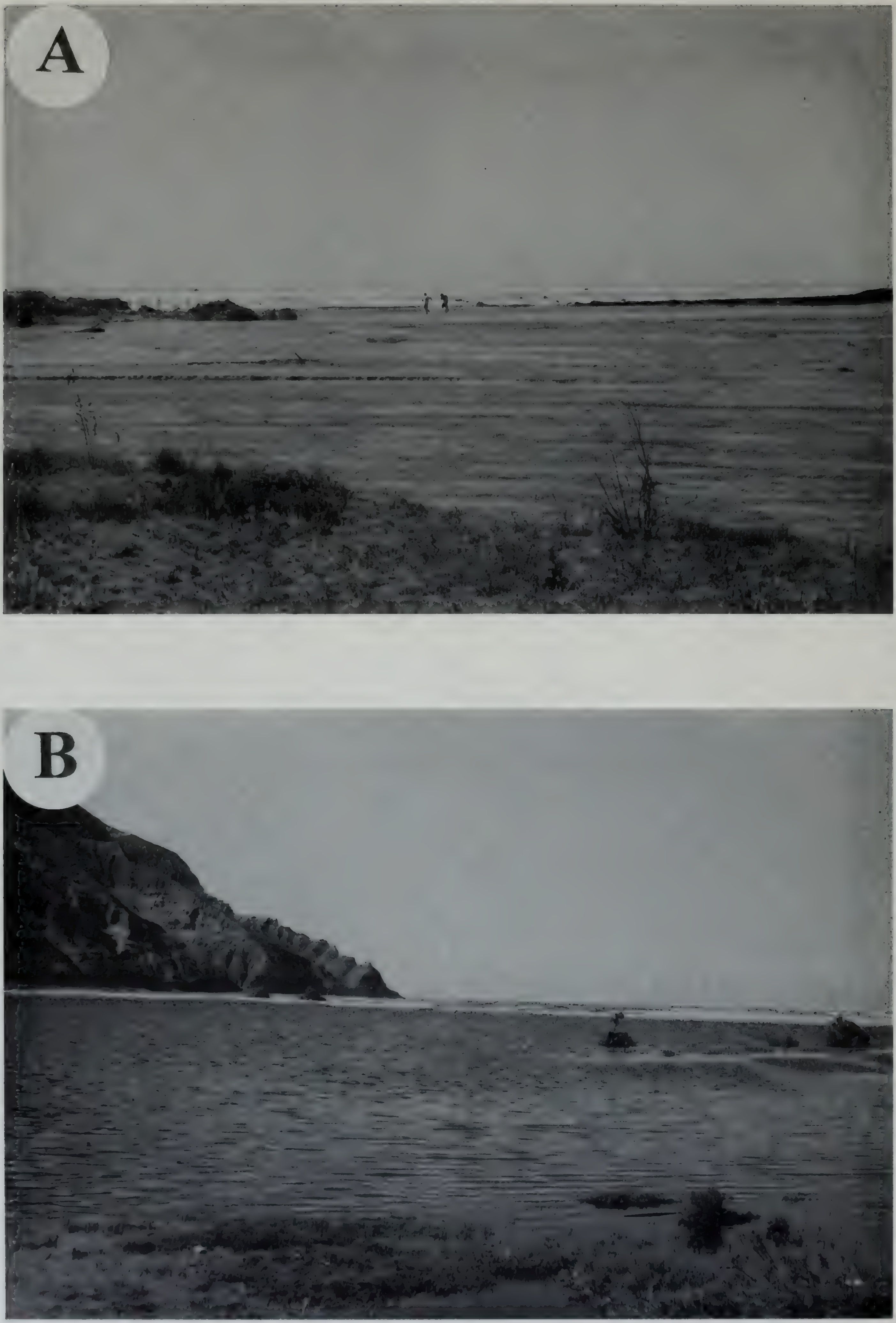

Fig. 3. (A) lower part of Arroyo Santo Domingo. (B) lower part of Arroyo El Rosario.

Table 1. Average values of physical-chemical parameters registered in the lower parts of the streams of the northwest of Baja California, México. Measurements made with Hydrolab scout 2.

Locality (stream)	Temp. °C	Salini. ppt	Oxyg. mg/l	pH	TDS g/l	Cond. mS/cm	Time	Date d/m/y
Cantamar (El Médano)	23.45	2.2	13.02	7.94	7.94	4.03	13:15	27-IV-1996
Cantamar (El Médano)	27.83	3.2	SS	8.35	3.62	5.71	15:00	21-VIII-1996
Cantamar (El Médano)	18.44	2	3.45	8.95	2.33	3.64	14:20	23-XI-1996
Cantamar (El Médano)	20.52	5.8	SS	8.31	6.1	10.04	10:40	20-III-1997
El Descanso (mouth)	18.73	13.4	4.2	8.69	14.25	22.27	14:15	22-XI-1996
El Descanso (mouth)	21.36	11.4	10.38	8.26	12.27	19.23	13:25	20-III-1997
El Descanso (slough)	23.95	6.8	4.78	8.4	7.05	12.04	12:10	27-IV-1996
El Descanso (slough)	30.5	11.3	SS	9.13	12.2	19.1	13:33	21-VIII-1996
El Descanso (slough)	18.39	9.5	3.04	9.13	10.41	16.31	12:14	22-XI-1996
El Descanso (slough)	18.52	10	10.57	8.85	10.96	17.09	13:00	4-IV-1997
La Misión (Guadalupe)	24.38	6.2	8.63	8.31	6.98	10.88	16:30	28-IV-1996
La Misión (Guadalupe)	25.46	9.5	6.46	8.2	10.4	16.2	12:00	21-VIII-1996
La Misión (Guadalupe)	18.37	8.4	5.38	9.25	9.33	14.5	12:24	23-XI-1996
La Misión (Guadalupe)	16.92	3.8	9.87	8.7	4.36	6.72	9:21	19-III-1997
San Miguel (El Carmen)	17.56	1.1	13.67	8.8	1.36	2.12	17:40	2-III-1994
San Miguel (El Carmen)	21.08	6.8	7.94	8.26	7.6	12.09	10:00	29-IV-1996
San Miguel (El Carmen)	16.69	13.1	5.1	9.78	14.05	21.98	11:00	29-XI-1996
San Miguel (El Carmen)	24.33	8.4	14.8	9.27	9.19	14.42	11:40	21-III-1997
Santo Tomás	NM	0.8	NM	7.96	0.94	1.46	15:30	24-III-1996
Santo Tomás	21.78	1.4	10.31	8.34	1.56	2.5	15:15	26-IX-1996
Santo Tomás	11.37	2.4	NM	8.11	NM	4.4	8:50	18-I-1997
San Vicente (Eréndira)	18.31	3.3	5.39	8.04	3.81	5.95	11:00	24-III-1996
San Vicente (Eréndira)	DS	DS	DS	DS	DS	DS	DS	28-IX-1996
El Salado (Loma Linda)	25.49	48.2	8.7	8.37	45.1	70.4	14:30	28-IX-1996
El Salado (Loma Linda)	17.81	25.9	8.04	8.52	NM	39.79	11:00	19-I-1997
San Rafael	21.04	51.9	7.23	7.86	48.6	75.7	11:00	23-III-1996
San Rafael	22.74	63.9	6.74	8.33	58.35	91.05	11:10	28-IX-1996
San Rafael	16.95	33.8	NM	8.35	NM	51.33	13:33	20-I-1997
Seco (tribut. San Rafael)	28.79	15.3	7.42	9.76	15.6	24.3	15:40	28-VI-1996
San Telmo	14.3	2.6	7.7	9.13	2.54	3.9	11:33	26-II-1996
San Telmo	28.04	5.3	7.64	8.74	6	9.36	13:12	28-VI-1996
San Telmo	24.89	1.74	9.23	8.76	2.05	3.21	14:45	13-X-1996
San Telmo	17.55	1.42	NM	8.47	NM	2.78	16:50	19-I-1997
Santo Domingo	18.99	2.6	8.96	9.21	3.03	4.72	11:56	25-II-1996
Santo Domingo	DS	DS	DS	DS	DS	DS	DS	27-VI-1996
Santo Domingo	DS	DS	DS	DS	DS	DS	DS	12-X-1996
Santo Domingo	DS	DS	DS	DS	DS	DS	DS	20-I-1997
San Simón (Papalote)	23.21	88	3.1	8.26	80.6	130	10:30	27-VI-1996
San Simón (Papalote)	16.52	32.4	4.8	8.37	31.7	49.52	10:00	7-III-1997
San Simón (La Pinta)	25.28	NM	6.06	9.98	22.5	35.1	16:25	27-VI-1996
San Simón (La Pinta)	24.37	4.9	7.54	7.84	5.58	8.74	13:38	12-X-1996
San Simón (La Pinta)	20.24	8.96	12.37	8.22	9.86	15.53	12:25	8-III-1997
El Rosario	16.19	14.4	4.62	8.84	14.97	21.65	24 Hs	24-II-1996
El Rosario	22.08	4.88	7.72	8.57	5.53	8.54	24 Hs	25-VI-1996
El Rosario	21.39	7.79	2.05	8.15	8.58	13.33	24 Hs	10-X-1996
El Rosario	15.56	19.88	7.63	7.97	20.39	31.91	24 Hs	8-III-1997

DS = dry streambed. NM = not measured.

were seasonally monitored during an annual cycle (February 1996 to March 1997) in order to determine the spatial and temporal distribution of the fish fauna.

In each locality a combination of passive (experimental gill nets, minnow traps) and active (minnow purse-seine and electrofishing) capture methods were used for the sampling of fishes at the different types of habitats. The same sampling effort was applied at each study locality. Electrofishing was used only in those streams with low salinities (< 1 ppt), such as the headwaters of streams.

Simultaneous to the fish sampling the physical-chemical variables of the water were measured *in situ* by using an Hydrolab Scout 2 (Hydrolab Co., Austin, Texas) multiparameter equipment (precision ± 0.01), which registered simultaneously temperature (°C), conductivity (mS/cm), dissolved oxygen (mg/l), potential of hydrogen ions (pH), salinity (ppt) and total dissolved solids (g/l).

The fish material was quantified and representative subsamples of the species were fixed in 10% formalin for subsequent preservation at 50% isopropanol in the laboratory. The rest of the specimens were measured (total length [TL] in mm) and returned to the original collecting site. Voucher specimens were deposited in the Fish Collections of the Facultad de Ciencias, Universidad Autónoma de Baja California (UABC) and the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (UANL).

The temporal occurrence of the species in the study area was classified as follows: *permanent residents,* those species collected throughout the year; *tidal visitors,* those peripheral species that penetrate stream mouths during high tides; and *occasional visitors,* species that appear incidentally in the mouths of streams and were represented by few collected specimens.

We provide each taxon with a synopsis that includes: known geographical range, previous and recent collecting records within the study area, bioecological data, ecological derivation, current status, and comments.

Previous records refers to collecting records for the study area published before 1983.

Recent records, include the records resulting of the present study (period of 1983 to 1997), which are supported with voucher specimens catalogued and deposited in the fish collections (UABC and UANL). The catalogue number(s) for each species is (are) given in parentheses, followed by the number of specimens in square brackets.

Bioecological data, includes relevant information about the taxon, such as preferential habitat, reproductive evidence in the continental waters, size classes, range of salinity and other data.

Ecological derivation, refers to the ecological category of the species according to its tolerance to salinity (cf. Myers 1938, 1951; Follett 1960): *diadromous,* species regularly migrant between fresh and salt water during a defined period of their life cycles; and *sporadic,* fishes that live and breed either in salt or fresh water or which enter fresh water only sporadically and not as a part of a true migration.

Conservation status, is based on periodic evaluations of the species distribution and abundance within the study region, as well as the condition of its habitats and the causative factors of its current population condition. The conservation categories used here are based on Williams et al. (1989) and SEDESOL (1994).

Comments, include diverse information about the distribution and abundance of the taxon in the study area or adjacent sites, or indicate the case of a new record for the continental waters of the State of Baja California and/or Peninsula of Baja California.

Results and Discussion

Species Accounts

A total of 23 fish species (19 native and 4 exotic) belonging to 22 genera, 15 families and 8 orders was registered for the study area during the period of 1983–1997. The taxonomical arrangement of the species follows Eschmeyer's (1998) classification. The common names of the species were based on Robins et al. (1991).

Native Taxa

Order Petromyzontiformes

Family Petromyzontidae

Lampetra tridentata (Gairdner, 1836). Pacific lamprey

Distribution.—Hokkaido, Japan through the Bering Sea and Aleutian Islands (Hart 1973) to Punta Canoas, Baja California, México (Hubbs 1967; Miller and Lea 1972). The previous southernmost known freshwater record is the lower Rio Santo Domingo [= San Ramón], Baja California (Ruiz-Campos and González-Guzmán 1996).

Previous records.—None.

Recent records.—Arroyo Santo Domingo ca. 600 m above its confluence to the Pacific Ocean (UABC-111 [1]) (Ruiz-Campos and González-Guzmán 1996), and Arroyo San Antonio (a third-order tributary of the Arroyo Santo Domingo) ca. 30 m before its confluence with Arroyo La Zanja, Sierra San Pedro Mártir (UABC-597 [1]).

Bioecological data.—The ammocoete of 126.5 mm TL from the lower Arroyo Santo Domingo (19-II-1995), was collected in a branch of the stream 5 m wide, 0.4 m deep, and over sand/gravel, with salinity of 0.3 ppt. The second ammocoete (92.5 mm TL) was collected (16-V-1997) in the sandy bottom of the Arroyo San Antonio, ca. 45 km upstream from the mouth of the Arroyo Santo Domingo, at salinity of 0.2 ppt.

Ecological derivation.—Diadromous.

Conservation status.—Special concern.

Comments.—The specimen UABC-597 is the second known fish species (after *Oncorhynchus M. nelsoni*) in the Sierra San Pedro Mártir. It is syntopical with the endemic trout, in the Arroyo San Antonio ca. Rancho San Antonio. The two findings of Pacific lamprey in the fresh waters of Baja California confirm once again the strong ichthyo-geographical affinity of the northwestern Baja California region with that of southern California (Swift et al. 1993). The presence of ammocotes in the middle Arroyo San Antonio suggests a connection of this stream with the ocean during high winter floods, when anadromous adults penetrate to the stream to spawn.

Order Clupeiformes
Family Engraulidae
Anchoa compressa (Girard, 1858). Deepbody anchovy

Distribution.—Morro Bay, California (U.S.A.) to Bahía Todos Santos, Baja California, México (Miller and Lea 1972; Fitch and Lavenberg 1975).

Previous records.—None.

Recent records.—Mouth of the Arroyo La Misión [= Guadalupe] (UABC-864 [1]).

Bioecological data.—The only specimen was collected along with a barred surfperch near the mouth of the stream, during the arrival of high tide flows (20 March 1995). The deepbody anchovy is commonly found in southern California bays and estuaries, where it prefers inshore and channel habitats (Horn and Allen 1985; Horn 1988).

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—The specimen registered here constitutes the first continental occurrence in the peninsula of Baja California.

Order Salmoniformes
Family Salmonidae
Oncorhynchus mykiss nelsoni (Evermann, 1908). San Pedro Mártir rainbow trout

Distribution.—Endemic to the Río Santo Domingo (= San Antonio de Murillos or San Ramón), Sierra San Pedro Mártir (SSPM), Baja California, México (Evermann 1908; Nelson 1921; Snyder 1926; Needham 1938; Smith 1991).

Previous records.—Arroyo Santo Domingo ca. Rancho San Antonio (type locality) in June 1902 (Meek 1904), 30 July 1905 (Evermann 1908; Nelson 1921), 24–27 April 1925 (Snyder 1926), 17 May 1936, 23 May 1937 (Needham 1938), and 14 May 1938 (Needham 1955).

Recent records.—Arroyo Santo Domingo ca. Rancho San Antonio (UABC-097 [11], 144 [10]), Arroyo La Zanja ca. junction with Arroyo San Antonio (UABC-143 [3]), Arroyo El Potrero at Rancho El Potrero (UABC-145 [4], 735 [1], 834 [8]), Arroyo La Grulla at La Grulla meadow (UABC-069 [7], 157 [17], 835 [21], 859 [6], 860 [3]; UANL-5679 [2]), Arroyo San Rafael at Rancho Mike's Sky (UABC-098 [1], 099 [4], 102 [30], 103 [43], 150 [1]), 841 [15], 842 [13], 843 [33], 844 [17], 845 [12], 846 [12], 847 [28], 848 [15], 849 [8], 850 [31], 851 [11], 852 [32], 853 [14], 854 [26], 855 [9], 856 [45], 857 [10], 858 [19], 861 [58]) and Arroyo San Rafael at Rancho Garet (UABC-148 [3], 149 [7], 151 [1], 152 [3]).

Bioecological data.—This rainbow trout is non-migratory and short lived (<5 years), and is distributed in the streams of the western slope of the Sierra San Pedro Mártir at elevations from 540 to 2,030 m. Preferred habitats are pools with depth >30 cm, heavy riparian and aquatic vegetation (*Ceratophyllum demersum* and *Potamogeton natans*), sandy bottoms, high availability of prey and salinities of 0.1 to 0.3 ppt (Ruiz-Campos and Pister 1995). The species' spawning period occurs between January and March and it is sexually mature at 103 mm standard length [SL] and after 1 year of age (Ruiz-Campos 1993). Newly emerged trout enter the population from May to June (Ruiz-Campos et al. 1997). *O. mykiss* *nelsoni* is sympatric with Pacific lamprey in the Arroyo Santo Domingo (Rancho San Antonio) ca. 45 km upstream from its mouth at the Pacific Ocean.

Ecological derivation.—Diadromous.

Conservation status.—Stable.

Comments.—The original distribution of this subspecies was a section of the Arroyo Santo Domingo from the Rancho San Antonio to 24 km upstream (Evermann 1908; Nelson 1921; Snyder 1926; Needham 1938, Smith 1991; Ruiz-Campos and Pister 1995). It was introduced into other streams of the western slope of the Sierra San Pedro Mártir between 1929 and 1941, such as La Grulla, La Zanja, La Misión [of San Pedro Mártir], El Potrero [= Valladares] and San Rafael (Ruiz-Campos and Pister 1995). Recent genetic analysis (mtDNA) confirmed the relationship of *O. mykiss nelsoni* with anadromous coastal trout (steelhead) from southern California (Nielsen et al. 1996; Nielsen 1998).

Order Atheriniformes
Family Atherinidae
Atherinops affinis (Ayres, 1860). Topsmelt

Distribution.—Vancouver Island [6.4 km W Sooke Harbour], British Columbia, Canada to Gulf of California (Miller and Lea 1972).

Previous records.—None.

Recent records.—Lower parts of the coastal streams of La Misión (UABC-074 [12], 127 [25], 198 [21], 431 [5], 482 [16], 591 [19], 596 [6]; UANL-13721 [13]), San Miguel (UABC-210 [9], 212 [5], 361 [6]), Santo Tomás (UABC-453 [7], 538 [2]) and El Rosario (UABC-101 [1], 465 [2], 593 [29]).

Bioecological data.—Topsmelts are found in small aggregations in main stream channels near their mouths. Gravid adults were observed from middle March to late May. This species was found in salinities ranging from 1.0 a 26.2 ppt. The most abundant populations were detected in the lower La Misión, San Miguel [= El Carmen o San Antonio de las Minas] and El Rosario streams.

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—All records referred above constitute the first occurrence of the species in the inland waters of the peninsula of Baja California. This species is known to enter inland waters of low salinity for spawning (Swift et al. 1993).

Atherinopsis californiensis Girard, 1854. Jacksmelt

Distribution.—Yaquina, Oregon, U.S.A. to Bahía Santa María, Baja California, México (Roedel 1953; Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouth of the streams of San Rafael (UABC-173 [35]) and La Misión (UABC-866 [11]).

Bioecological data.—This species was represented by juveniles that were captured along with longjaw gobies in two isolated hypersaline ponds (38.8 and 51.9 ppt) at the mouth of Arroyo San Rafael, which is blocked of the sea by a wide bar of boulders.

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—The finding of jacksmelt in the mouths of the streams of La Misión and San Rafael, represents the first mainland records in the peninsula of Baja California.

Leuresthes tenuis (Ayres, 1860). California grunion

Distribution.—San Francisco, California, U.S.A. to Bahía Magdalena, Baja California Sur (Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouths of the streams of San Miguel (UABC-142 [121]) and La Misión (UABC-867 [1]).

Bioecological data.—Two adults and 119 juveniles were caught (30 June 1995) in a small lagoon near the mouth of the stream at San Miguel, which is blocked from the ocean by a sandy bar. Juveniles of this taxon have been reported from rocky tide pools near the collecting site (Ruiz-Campos and Hammann 1987).

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—An adult specimen (UABC-867) was collected on 8 June 1995 in the mouth of Arroyo La Misión during the entry of tidal flows (Cabrera-Santillán 1997).

Family Fundulidae

Fundulus parvipinnis parvipinnis Girard, 1854. California killifish

Distribution.—Morro Bay, California, U.S.A. (Miller and Lea 1972) to Ojo de Liebre lagoon, Baja California Sur, México (De La Cruz-Agüero et al. 1996).

Previous records.—Lower parts of the coastal streams of Cantamar [= Médano], La Misión and San Miguel (Miller 1943; Follett 1960).

Recent records.—Lower parts of the coastal streams of Cantamar (UABC-350 [64], 437 [92], 446 [80], 469 [116], 479 [7], 595 [22]; UANL-13724 [94]), El Descanso (UABC-141 [66], 358 [4], 407 [2], 478 [16], 484 [12], 485 [34], 505 [4], 590 [14]), La Misión (UABC-072 [29], 128 [16], 155 [28], 360 [242], 418 [3], 432 [46], 447[160], 480 [4], 483 [1], 589 [1]; UANL-13719 [13]), San Miguel (UABC-213 [1], 221 [1]) and San Simón (UABC-316 [17], 587 [63]; UANL-2536 [43]). This species was also recorded in a slough adjacent to the mouth of Arroyo El Descanso (UABC-434 [2], UANL-13722 [1]).

Bioecological data.—This euryhaline and sporadic killifish prefers the littoral habitats of sandy or muddy bottom such as marsh pools and inshores. It was registered within a wide range of salinity (1.0 to 88 ppt). Sexually ripe individuals were detected between April and May. California killifish is very abundant in the northern streams of the study area (e.g., Cantamar, La Misión and El Descanso) but absent from south of Arroyo San Miguel to Arroyo Santo Domingo. Three age-classes (0–2 years) were identified according to Fritz's (1975) criterion: Juvenile (< 44 mm SL), 1 year (44–79 mm SL) and 2 years (> 79 mm SL). Juveniles were observed from March to November.

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—This taxon is one of the most typical and abundant species of marshes and esturies of southern California (Horn 1988) and some coastal lagoons of the peninsula of Baja California (Ojo de Liebre and Guerrero Negro; De La

Cruz-Agüero et al. 1996). Its euryhaline capacity allows it to be the dominant species at mixohaline systems (mouths) subject to flooding by high tides.

Order Gasterosteiformes
Family Gasterosteidae
Gasterosteus aculeatus microcephalus Girard, 1854. Partially armored threespine stickleback

Distribution.—Bering Strait, Alaska (Eigenmann 1886) to Arroyo El Rosario, Baja California, México (Follett 1960).

Previous records.—"Tía Juana Hot Springs" [= Manantiales Agua Caliente] (Smith 1883), Wild Cat stream [= Arroyo Gato Bronco] (Smith 1883), lower parts of the coastal streams of Cantamar, El Descanso, Guadalupe [= Matanyonal or La Misión], Santo Tomás, San Vicente, Seco [tributary of Arroyo San Rafael] (Miller and Hubbs 1969), El Salado (= San Antonio del Mar) (Rutter 1896), Santo Domingo (Myers 1930; Swift et al. 1993) and El Rosario (Follett 1960).

Recent records.—Mouth of the coastal streams of El Descanso (UABC-070 [12], 410 [18]), Santo Domingo (UABC-165 [39], 167 [1], 168 [37]) and El Rosario (UABC-113 [1], 163 [174], 307 [22], 459 [1], 583 [77], 585 [1]). An additional record is that of a slough near the mouth of Arroyo El Descanso (UABC-199 [5], 200 [23], 436 [52], UANL-13723 [36]).

Bioecological data.—Threespine sticklebacks inhabit those sites with marginal emergent (bulrush, *Scirpus californicus* and cattail, *Typha domingensis*) or submergent aquatic vegetation, with sandy and silty bottoms. This species was found at salinities of 1.0 to 15.6 ppt (mean= 6.7). It is sympatric with exotic mosquitofish (*Gambusia affinis*). Ripe adults were observed from November to April, and newly transformed juveniles between March and May. The population of the slough near the mouth of Arroyo El Descanso (Fig. 2a) makes up the most abundant and permanent stock in northwestern Baja California. Three age-classes were recognized (0–2 years old) according to Carlander's (1969) criterion: juvenile (< 28 mm TL), 1 year (28–60 mm TL) and 2 years (> 60 mm TL). Juveniles were distinguished from February to June.

Ecological derivation.—Diadromous.

Conservation status.—Threatened. This taxon was considered rare by SEDESOL (1994) based on old collecting records. Its population is being reduced.

Comments.—This subspecies once widely distributed in the coastal streams of northwestern Baja California is now confined to three localities. This distributional reduction is associated to alteration of habitats by man-made impacts (e.g., urbanization, pollution, livestock grazing and siltation), being most evident along the Tijuana-Ensenada tourist corridor and the agricultural valleys of San Quintín and Colonet.

Order Scorpaeniformes
Family Cottidae
Leptocottus armatus australis Hubbs, 1921. Pacific staghorn sculpin

Distribution.—Morro Bay, California, U.S.A. (Hubbs 1921) to Bahía San Quintín, Baja California, México (Bolin 1944; Follett 1960; Miller and Lea 1972).

Previous records.—Arroyo Rosarito (Smith 1883) and Arroyo Guadalupe (La Misión) (Follett 1960).

Recent records.—Lower parts of the coastal streams of Cantamar (UABC-209 [12]), La Misión (UABC-067 [1], 868 [8]), San Miguel (UABC-082 [1]) and Santo Tomás (UABC-219 [1]).

Bioecological data.—The presence of this sculpin in the coastal streams of the study area is concomitant to the opening of their mouths by high freshwater flows. Adult specimens (90.1–191 mm TL) were collected in salinities ranging of 0.8 to 2.2 ppt.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—Our record of *L. armatus australis* in the lower Arroyo Santo Tomás, extends approximately 66 km southward the previously known freshwater range (Arroyo La Misión, cf. Follett 1960).

Order Perciformes

Family Kyphosidae

Girella nigricans (Ayres, 1860). Opaleye.

Distribution.—Otter Rock [Lincoln county], Oregon, U.S.A. (Bond 1985) to Punta Entrada, Bahía Magdalena, Baja California Sur, México (Norris 1963).

Previous records.—None.

Recent records.—Mouths of the coastal streams of La Misión (UABC-871 [1]) and San Miguel (UABC-197 [1], 214 [1], 200 [6]).

Bioecological data.—Subadult fish were collected in the mouth of the stream during intromision of tidal flows, at salinities of 6.3 to 7.3 ppt. Juveniles are common in the rocky tide pools near the mouth (Ruiz-Campos and Hammann 1987).

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—The finding of this coastal species in the streams of La Misión and San Miguel constitute their first inland records in the Baja California peninsula.

Family Mugilidae

Mugil cephalus Linnaeus, 1758. Striped mullet

Distribution.—Circumtropical species, also distributed in many temperate regions (boundary of 15 °C-surface isotherm). In the Eastern Pacific Ocean it occurs from Monterey, California (Miller and Lea 1972) to Chile (Puerto Montt), including Gulf of California and Galápagos Islands (Harrison 1995).

Previous records.—Arroyo La Misión 1.6 km E Pacific Ocean (Follett 1960) and Arroyo San Simón ca. 4 km W Lázaro Cárdenas (Ruiz-Campos and Contreras-Balderas 1987).

Recent records.—Lower parts of the streams of Cantamar (UABC-450 [2]), El Descanso [adjacent slough] (UABC-208 [1]), 957 [1], La Misión (UABC-118 [1], 449 [2]), San Miguel (UABC-083 [11]), Santo Tomás (UABC-211 [3], 451 [6]), El Salado (UABC-467 [1], 549 [2]), San Rafael (UABC-548 [2]), San Telmo (UABC-170 [5], 313 [16]), Santo Domingo (UABC-112 [136]), San Simón (UANL-2538 [19]), and El Rosario (UABC-120 [294], 139 [2], 159 [46], 161 [3], 315 [2], 448 [19], 461 [12], 594 [3]).

Bioecological data.—This euryhaline species (0.3 to 48.3 ppt) prefers the main channels of streams near their mouths, where high dynamics exist due to tidal inflows. Subadult striped mullets (<150 mm TL) were seen 20 km upstream from the mouth of Arroyo Santo Tomás (21 June 1998). Young-of-the-year (YOY) individuals were collected in February. Two adults (460 and 535 mm TL) were netted in an isolated slough near the mouth of Arroyo El Descanso (Fig. 2a), which is separated from the ocean by a wide bar of sand and boulder that can hardly be surpassed by high tides. Both specimens had abundant mesenterial fat and degenerate gonads that suggest suppression of breeding migration because of the spatial isolation.

Ecological derivation.—Diadromous.

Current status.—Stable.

Comments.—It is one of the most widespread species in the study area (Table 2) with abundant populations in the lower parts of La Misión and El Salado streams.

Family Embiotocidae

Amphistichus argenteus Agassiz, 1854. Barred surfperch

Distribution.—Bodega Bay, California, U.S.A. to mouth of Arroyo La Misión, Baja California, México (Tarp 1952).

Previous records.—Mouth of Arroyo La Misión (Tarp 1952).

Recent records.—Mouth of Arroyos La Misión (UABC-863 [1]) and El Rosario (UABC-466 [13]).

Bioecological data.—Juveniles and adults (131-346 mm TL) were captured in the main channel of Arroyo El Rosario ca. 80 m above mouth, during tidal inflow (salinity of 24.6 ppt). This surfperch is commonly caught by hook and line in the sublittoral adjacent to the collecting site.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—The record of the species in the mouth of Arroyo El Rosario, represents its southernmost locality.

Hyperprosopon argenteum Gibbons, 1854. Walleye surfperch

Distribution.—Vancouver Island, British Columbia, Canada to Punta San Rosarito, Baja California, México (Tarp 1952; Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouth of the Arroyo El Rosario (UABC-457 [1], cf. comments, *infra*).

Bioecological data.—The only specimen registered here (197 mm TL) was captured along with adult and juvenile barred surfperch near the mouth of the stream, during the inflow of tidal currents (salinity of 24.6 ppt).

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—The specimen reported here represents the first finding of the species in the continental waters of the peninsula of Baja California.

Micrometrus minimus Gibbons, 1854. Dwarf perch

Distribution.—Bodega Bay, California, U.S.A. (Tarp 1952) to Isla de Cedros, Baja California, México (Miller and Lea 1972).

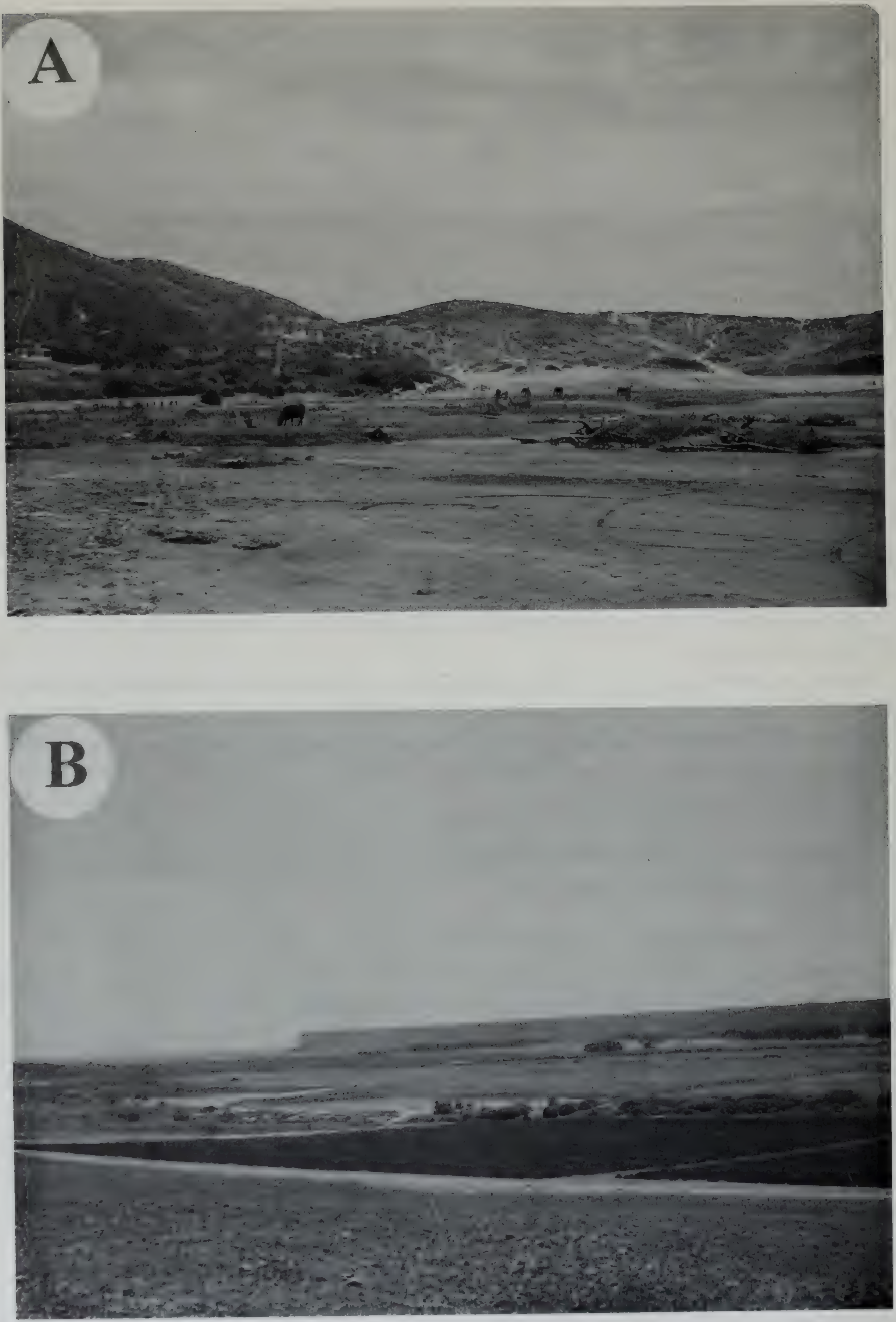

Fig. 4. (A) Livestock grazing in the riparian biotopes in the lower part of Arroyo Santo Tomás. (B) Modification of sites adjacent to the lower part of Arroyo San Rafael for intensive agriculture practices.

Previous records.—None.

Recent records.—Mouth of Arroyo San Miguel (UABC-081 [1]).

Bioecological data.—The only specimen was captured on March 3 1994, in the mouth of the Arroyo El Carmen, which is blocked from the ocean by a sandy bar. This species was detected in salinity of 1.1 ppt.

Ecological derivation.—Sporadic.

Conservation status.—Stable.

Comments.—The specimen reported here is the first occurence of this species in the continental waters of the peninsula Baja California, and at strictly oligohaline conditions.

Family Gobiidae

Clevelandia ios (Jordan & Gilbert, 1882). Arrow goby

Distribution.—Vancouver Island, British Columbia, Canada to Gulf of California (Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouth of Arroyo San Rafael (UABC-175 [8], 176 [3]).

Bioecological data.—Juvenile arrow gobies were found in two isolated hypersaline ponds (51.9 ppt) with dense submergent macrophytes near the mouth of the stream.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—This goby has not been previously reported in the mainland Baja California.

Ilypnus gilberti (Eigenmann & Eigenmann, 1889). Cheekspot goby

Distribution.—Walker stream, Tomales Bay (California, U.S.A.) to Gulf of California (Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouth of Arroyo Santo Domingo (UABC-164 [1]).

Bioecological data.—The only specimen was collected in a remnant pond (salinity of 2.6 ppt) on the stream's dry bed, which is located ca. 600 m above mouth. It is syntopic with longjaw mudsucker, threespine stickleback and mosquitofish.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—In spite of the presence of this goby in Bahía San Quintín (Rosales-Casián 1996), it had not been previously reported from the continental waters of Baja California.

Gillichthys mirabilis Cooper, 1864. Longjaw mudsucker

Distribution.—Tomales Bay, California, U.S.A. to Gulf of California (Miller and Lea 1972).

Previous records.—Mouth of Arroyo San Simón, ca. 4 km W Lázaro Cárdenas (Ruiz-Campos and Contreras-Balderas 1987).

Recent records.—Lower parts of the Arroyos La Misión (UABC-068 [1], 126 [1], 215 [11], 406 [14], 429 [1], 486 [1], 489 [3], 869 [1]), El Salado (UABC-454 [98], 464 [5], 537 [11]), San Rafael (UABC-171 [16], 172 [36], 174 [6], 470

[23], 539 [25]), Santo Domingo (UABC-598 [3]) and San Simón (La Pinta: UABC-319 [159], 460 [252], 456 [7], 586 [3]; and Papalote: UABC-314 [11], 588 [4], UANL-2539 [427]).

Bioecological data.—This euryhaline species (salinity range = 4.9 to 88 ppt) was commonly found on muddy bottoms of ponds and channels with abundant submerged vegetation. Most of the collected specimens were YOY (< 127 mm TL) and > 1 year old (152–178 mm TL).

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—Five new localities are added to the inland distribution of the species in Baja California.

Order Pleuronectiformes

Family Paralichthyidae

Hippoglossina stomata Eigenmann & Eigenmann, 1890. Bigmouth sole

Distribution.—Monterey Bay, California, U.S.A. to Gulf of California, including Isla Guadalupe (Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouth of Arroyo San Miguel.

Bioecological data.—The only specimen reported here was caught on April 29 1996 in a remaining pond (salinity of 6.8 ppt) near the mouth of the stream, which is closed by a sandy bar. The specimen was identified in the field in accordance with Miller and Lea (1972) and then released there.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—This record represents the first occurence of the taxon in the inland waters of the peninsula of Baja California.

Family Pleuronectidae

Hypsopsetta guttulata (Girard, 1856). Diamond turbot

Distribution.—Cape Mendocino, California, U.S.A. to Bahía Magdalena, Baja California Sur, México, with an isolated population in the Gulf of California (Miller and Lea 1972).

Previous records.—None.

Recent records.—Mouths of the streams of La Misión (UABC-433 [1], 468 [1]) and El Salado (UABC-463 [3]).

Bioecological data.—This euryhaline species was collected in the lower parts of streams with sandy bottoms during conditions of closing (8.4 ppt) or opening (48.2 ppt) of the mouth. In the lower Arroyo El Salado, three diamond turbots were collected 1 km above mouth.

Ecological derivation.—Sporadic.

Current status.—Stable.

Comments.—Our records of *H. guttulata* in the streams of La Misión and El Salado, constitute the first findings of the taxon in the continental waters of the State of Baja California.

Exotic Taxa

Order Atheriniformes

Family Poeciliidae

Gambusia affinis (Baird & Girard, 1853). Mosquitofish

Previous records.—Río Tijuana (3.2 km E Tijuana), Arroyo Guadalupe (= La Misión) in the Valle de Santa Rosa and town of La Misión (4.8 km E highway), and Arroyo San Simón S San Quintin (Follett 1960).

Recent records.—Mouth of Arroyo El Descanso (UABC-409 [14], 411 [710], 435 [7], 481 [6]); lower Arroyo La Misión (mouth: UABC-216 [2], 487 [7], UANL-13720 [8]; town: UABC-050 [3], 073 [9]; and Rancho Santa Rosa: UABC-376 [65]); mouth of Arroyo San Miguel (UABC-201 [10], 488 [99]); Arroyo Santo Tomás at Ejido Ajusco (UABC-605 [2]); Arroyo Seco ca. Colonet (UABC-317 [56]); mouth of Arroyo San Telmo (UABC-169 [61], 312 [315], 471 [26]), Arroyo Santo Domingo (ca. 600 m above mouth: UABC-166 [1], 310 [9]; and at rancho El Divisadero ca. Misión Santo Domingo: UABC-455 [112], 592 [30]); and lower Arroyo El Rosario (UABC-160 [2], 162 [30], 309 [14], 320 [56], 458 [130], 462 [12], 584 [32]).

Bioecological data.—This exotic poeciliid is widely distributed along the study area, including some localities in the Sierra de Juárez (Laguna Hanson and Arroyo Neji). It prefers lentic and shallow habitats with abundant submergent and emergent plants, and of sandy-muddy bottoms. In the lower parts of streams, this species is found at salinities ranging from 0.2 to 15.6 ppt.

Comments.—This ubiquitous taxon may be a current or potential competitor to the native fish, *Gasterosteus aculeatus microcephalus,* since both are syntopical in the lower parts of the streams of El Descanso, Santo Domingo and El Rosario.

Order Perciformes

Family Centrarchidae

Lepomis cyanellus Rafinesque, 1819. Green sunfish

Previous records.—Río Tijuana, 3.2 km E Tijuana; a stream entering to the southwestern corner of Valle de Santa Rosa, 32.2 km S [sic] Ensenada; and Arroyo San Miguel (Follett 1960).

Recent records.—An slough adjacent to the mouth of Arroyo El Descanso (UABC-177 [1]); Arroyo La Misión at its mouth (UABC-865 [1]), at Rancho Tierra Santa (UABC-665 [33]) and at Rancho Santa Rosa (UABC-377 [4]); Arroyo San Carlos at Rancho Alamitos (2 ripe males and 2 juveniles collected but not preserved, on 1 May 1995), Arroyo Santo Tomás near the mouth (UABC-452 [1]) and at Ejido Ajusco (UABC-224 [2]); mouth of Arroyo San Telmo (UABC-311 [6]), and Arroyo Santo Domingo at Rancho El Divisadero (G. Ruiz-Campos, pers. obs.).

Bioecological data.—Green sunfish prefer ponds with abundant submergent macrophytes (*Ceratophyllum demersum*) and sandy bottoms. Ripe adults were observed between April and May. It is coexisting with mosquitofish in many localities of the study area, within a salinity range of 0.4 to 6.9 ppt.

Comments.—The Follett's (1960) record from Valle de Santa Rosa corresponds to a personal communication by Dr. Carl L. Hubbs, who referred it to 32.2 km S Ensenada instead of 32.2 km N Ensenada.

The following two exotic species were captured in localities not considered for the spatial and temporal fish monitoring. These localities are within the study area and period:

Lepomis macrochirus Rafinesque, 1819. Bluegill

Previous records.—None.

Recent records.—Laguna Hanson, Sierra de Juárez (UABC-077 [4]) and Emilio López Zamora reservoir near Ensenada (UABC-415 [2]).

Comments.—The specimens from Laguna Hanson were reported incorrectly by Ruiz-Campos and Contrears-Balderas (1987) as *L. megalotis* instead of *L. macrochirus.*

Micropterus salmoides (Lacépède, 1802). Largemouth bass

Previous records.—None.

Recent records.—Emilio López Zamora reservoir near the city of Ensenada (UABC-413 [4]) and Laguna Hanson at Sierra Juárez (G. Ruiz-Campos, pers. obs.).

Comments.—This game fish has been recently stocked in several small bodies in the region in order to promote sport fishing.

Ecological Composition

The spatial and temporal composition of the ichthyofauna was evaluated during an annual cycle (February 1996 to March 1997) along twelve coastal streams of the study area (Fig. 1).

Two species (*Mugil cephalus* and *Gambusia affinis*) were recorded from most coastal streams of the area, occurring in ten and seven streams, respectively (Table 2). Other species with wide distribution were: *Fundulus p. parvipinnis* (5 streams), *Gillichthys mirabilis* (5), *Lepomis cyanellus* (5), *Atherinops affinis* and *Leptocottus armatus australis* (4 each). The rest of the taxa were restricted to less than four streams in the study area. The Arroyo San Vicente (lower part) was the only sampled locality that no had fish.

In relationship to the temporal occurrence of the species, eight (34.8%) were permanent residents: *Oncorhynchus mykiss nelsoni, Fundulus p. parvipinnis, Gasterosteus aculeatus microcephalus, Mugil cephalus, Gambusia affinis, Lepomis cyanellus, Lepomis macrochirus,* and *Micropterus salmoides*; nine (39.1%) were tidal visitors: *Atherinops affinis, Atherinopsis californiensis, Leuresthes tenuis, Leptocottus armatus australis, Girella nigricans, Amphistichus argenteus, Clevelandia ios, Gillichthys mirabilis,* and *Hypsopsetta guttulata*; and six (26.1%) occasional visitors: *Lampetra tridentata, Anchoa compressa, Hyperprosopon argenteum, Micrometrus minimus, Ilypnus gilberti,* and *Hippoglossina stomata.*

The most abundant fish species during the seasonal samplings were *F. parvipinnis parvipinnis, Atherinops affinis, Gillichthys mirabilis, Mugil cephalus* and *Gasterosteus aculeatus microcephalus* (Table 3). With the exception of *G. microcephalus,* a diadromous species, most of the abundant species are of sporadic and euryhaline type that penetrate the streams during high tides (Horn 1988; Zedler et al. 1992; Saiki 1997).

The widest intervals of salinity were recorded for *F. parvipinnis parvipinnis, Atherinops affinis, Mugil cephalus, Clevelandia ios, Gillichthys mirabilis,* and

Table 2. Distribution of the fish species collected in the middle and lower parts of the streams of northwestern Baja California, México (1995–1997 period). Abbreviations: CM = Cantamar, DE = El Descanso, LM = La Misión, EC = El Carmen, ST = Santo Tomás, SV = San Vicente, ES = El Salado, SR = San Rafael, TE = San Telmo, SD = Santo Domingo, SS = San Simón, and ER = El Rosario.

	Localities												
Taxa	CM	DE*	LM	EC	ST	SV	ES	SR°	TE	SD	SS**	ER	Total
Lampetra tridentata										X			1
Anchoa compressa			X										1
Oncorhynchus mykiss nelsoni								X		X			2
Fundulus parvipinnis parvipinnis	X	X	X	X							X		5
Atherinops affinis			X	X	X							X	4
Atherinopsis californiensis			X					X					2
Leuresthes tenuis			X	X									2
Gasterosteus aculeatus microcephalus		X								X		X	3
Leptocottus armatus australis	X		X	X	X								4
Girella nigricans			X	X									2
Amphistichus argenteus			X									X	2
Hyperprosopon argenteum												X	1
Micrometrus minimus				X									1
Mugil cephalus	X	X	X	X	X		X	X	X	X		X	10
Clevelandia ios								X					1
Ilypnus gilberti										X			1
Gillichthys mirabilis			X				X	X		X	X		5
Hippoglossina stomata				X									1
Hypsopsetta guttulata			X				X						2
Gambusia affinis		X	X	X				X	X	X		X	7
Lepomis cyanellus		X	X		X				X	X			5
Total	3	5	13	9	4	0	3	6	3	8	2	6	

* Include the adjacent slough.

** Localities of Papalote and La Pinta combined.

° Include its tributary Arroyo Seco ca. Colonet.

Table 3. Temporal abundance of fish species collected in the lower parts of streams of northwestern Baja California, México.

Arroyo Cantamar

Taxa	27-IV-1996	21-VIII-1996	23-XI-1996	20-III-1997	Total	%
Fundulus parvipinnis parvipinnis	342	188	7	*	537	96.6
Leptocottus armatus australis	12	1		*	13	2.3
Mugil cephalus		6		*	6	1.1
Total	354	195	7	*	556	

* = Absence of fish.

Arroyo El Descanso*

Taxa	27-IV-1996	21-VIII-1996	22-XI-1996	20-III-1997	Total	%
Fundulus parvipinnis parvipinnis		2		14	16	3.4
Gasterosteus aculeatus microcephalus	129	52	128	124	433	93.3
Mugil cephalus	2	1	3		6	1.3
Gambusia affinis		7	1		8	1.7
Lepomis cyanellus	1				1	0.3
Total	132	62	132	138	464	

* Include the adjacent slough.

Arroyo La Misión

Taxa	28-IV-1996	21-VIII-1996	23-XI-1996	19-III-1997	Total	%
Fundulus parvipinnis parvipinnis	160	46	1	1	208	29.8
Atherinops affinis	21	60	145	211	437	62.7
Mugil cephalus		2	4	1	7	1
Gillichthys mirabilis	25	1	1		27	3.9
Hypsopsetta guttulata		1	1		2	0.3
Gambusia affinis	2	7	7		16	2.3
Total	208	117	159	213	697	

Table 3. Continued.

Arroyo El Carmen

Taxa	2-III-1994	29-IV-1996	29-XI-1996	Total	%
Fundulus parvipinnis parvipinnis		2		2	1.1
Atherinops affinis	6	36		42	24
Leptocottus armatus australis	1			1	0.6
Girella nigricans		8		8	4.6
Micrometrus minimus	1			1	0.6
Mugil cephalus	11			11	6.3
Hippoglossina stomata		1		1	0.6
Gambusia affinis		10	99	109	62.2
Total	19	57	99	175	

Arroyo Santo Tomás

Taxa	30-VI-1995	24-III-1996	26-IX-1996	18-I-1997	Total	%
Atherinops affinis			6	2	8	24.3
Leptocottus armatus australis		1			1	3
Mugil cephalus	15	3	5		23	69.7
Lepomis cyanellus			1		1	3
Total	15	4	12	2	33	

Arroyo El Salado

Taxa	28-IX-1996	19-I-1997	Total	%
Mugil cephalus	13	5	18	48.6
Gillichthys mirabilis	5	11	16	43.2
Hypsopsetta guttulata	3		3	8.2
Total	21	16	37	

Table 3. Continued.

Arroyo San Rafael

Taxa	23-III-1996	28-IX-1996	20-I-1997	Total	%
Atherinopsis californiensis	35	23		58	55.8
Mugil cephalus			4	4	3.8
Clevelandia ios	11			11	10.6
Gillichthys mirabilis	6		25	31	29.8
Total	52	23	29	104	

Arroyo San Telmo

Taxa	26-II-1996	28-VI-1996	13-X-1996	19-I-1997	Total	%
Mugil cephalus	5	16		*	21	4.9
Gambusia affinis	61	315	26	*	402	93.7
Lepomis cyanellus		6		*	6	1.4
Total	66	337	26	*	429	

* = Absence of fish.

Arroyo Santo Domingo

Taxa	19-II-1995	25-II-1996	27-VI-1996	12-X-1996	20-I-1997	Total	%
Lampetra tridentata	1		DS	DS	DS	1	0.5
Gasterosteus aculeatus microcephalus		77	DS	DS	DS	77	35.1
Mugil cephalus	136		DS	DS	DS	136	62.1
Ilypnus gilberti		1	DS	DS	DS	1	0.5
Gillichthys mirabilis		3	DS	DS	DS	3	1.3
Gambusia affinis		1	DS	DS	DS	1	0.5
Total	137	82	0	0	0	219	

DS = Dry streambed.

Table 3. Continued.

Arroyo San Simón*

Taxa	27-VI-1996	12-X-1996	7-III-1997	Total	%
Fundulus parvipinnis parvipinnis	17		63	80	15.5
Gillichthys mirabilis	170	259	7	436	84.5
Total	187	259	70	516	

* The localities of Papalote and La Pinta combined.

Arroyo El Rosario

Taxa	18-II-1995	24-II-1996	25-VI-1996	10-X-1996	8-III-1997	Total	%
Atherinops affinis				2	108	110	10.8
Gasterosteus aculeatus microcephalus	1	174	22	1	77	275	27.1
Amphistichus argenteus				21		21	2.1
Hyperprosopon argenteum				1		1	0.1
Mugil cephalus	294	49	27	23	7	400	39.4
Gambusia affinis		32	14	130	32	208	20.5
Total	295	255	63	178	224	1015	

Hypsopsetta guttulata, which are typical representatives of the euryhaline marine component (Castro-Aguirre 1978). Other species as *Lampetra tridentata, Leptocottus armatus australis, Gambusia affinis* and *Lepomis cyanellus,* were associated with low salinity levels.

Species similarity among streams was significantly low in most of the cases (Table 4), with the exception of the Arroyos El Descanso and San Telmo that registered a similarity of 60%. The low similarity of species was associated to localities with high seasonal variation in the species composition.

The ecological classification of the native continental fish species of northwestern Baja California, which is based on their tolerance to salinity (Myers 1938; Follett 1960), includes 15 sporadic (78.9%) and four diadromous species (21.1%) (cf. synopsis). This demonstrates the complete dominance in inland waters by fish forms of marine derivation. This situation of dominance is typical of recently emerged geographical regions (e.g., Central America and Caribbean islands) (Myers 1938, 1951; Miller 1966), which are colonized by marine species that enter the mouths of streams, and some of them as *Lampetra tridentata* and *Mugil cephalus,* can penetrate as far as 45 and 23 km upstream, respectively.

Ichthyogeography

Of 19 native taxa, 13 (68.4%) are of Californian affinity: *Anchoa compressa, Fundulus p. parvipinnis, Atherinops affinis, Atherinopsis californiensis, Leuresthes tenuis, Leptocottus armatus australis, Girella nigricans, Amphistichus argenteus, Micrometrus minimus, Ilypnus gilberti, Gillichthys mirabalis, Hippoglossina stomata,* and *Hypsopsetta guttulata,* three (15.7%) are of the eastern Pacific of North America (*Gasterosteus aculeatus microcephalus, Hyperprosopon argenteum* and *Clevelandia ios*), one Holarctic (5.3%, *Lampetra tridentata*), one Endemic (5.3%, *Oncorhynchus mykiss nelsoni*) and one Circumtropical (5.3%, *Mugil cephalus*).

The number of fish species registered in the present study is quite lower than that reported for the continental waters of southern California (Swift et al. 1993), where a greater quantity of perennial streams exist. Two main causes explain the low richness of fish species in the northwestern Baja California (Follett 1960): (1) its great aridity that results in few perennial streams; and (2) a paleohydrological discontinuity between the streams of southern California and those of northern Baja California.

In our region of study, there are seven taxa that reach their southernmost continental ranges (cf. Tarp 1952; Follett 1960; Miller and Lea 1972): *Lampetra tridentata, Oncorhynchus mykiss, Fundulus p. parvipinnis, Atherinopsis californiensis, Gasterosteus aculeatus microcephalus, Leptocottus armatus australis,* and *Amphistichus argenteus.* The presence of holarctic diadromous taxa (*L. tridentata, O. mykiss* and *G. aculeatus*) as far south as Arroyo El Rosario supports Nelson's (1921) hypothesis that the vicinity of El Rosario is the southern boundary of the San Diegan faunal district.

Four exotic species were registered in this study (*Gambusia affinis, Lepomis cyanellus, L. macrochirus* and *Micropterus salmoides*), of which *G. affinis* is of wide distribution in the region and coexists with the native threespine stickleback (*G. aculeatus microcephalus*) in the lower parts of El Descanso (slough), Santo Domingo and El Rosario streams.

Table 4. Percent of species similarity (Jaccard's index*) among coastal streams (lower parts) of northwestern Baja California, México (period: 1995–1997). All dates of collecting combined for each locality.

	Coastal streams										
	Cantamar	Descanso	La Misión	El Carmen	S. Tomás	El Salado	S. Rafael	S. Telmo	S. Domingo	S. Simón	El Rosario
Cantamar	100	33.3	23.1	33.3	40	20	12.5	20	10	25	11.1
Descanso		100	28.6	27.3	28.6	14.3	22.2	60	44.4	16.7	9.1
La Misión			100	46.7	30.8	23.1	26.7	23.1	23.5	15.4	26.7
El Carmen				100	30	9.1	15.4	20	13.3	10	33.3
S. Tomás					100	16.7	11.1	40	20	0	22.2
El Salado						100	28.6	20	22.2	25	11.1
S. Rafael							100	28.6	40	14.3	18.2
S. Telmo								100	37.5	0	25
S. Domingo									100	11.1	25
S. Simón										100	0
El Rosario											100

Significant similarity for values equal or higher than 60%.

* CCJ = c/[a + b − c]; where "a" and "b" are number of species in the streams "a" and "b", respectively; and "c" = number of species shared in both streams (Brower and Zar, 1977).

Conservation Status

Based on the fish samplings in the study area, most of collected species are determined to have a stable conservation status. However, three diadromous species were determined to have the following statuses: (1) *Lampetra tridentata,* was determined as special concern due to its recent records in the freshwater waters of Baja California (Ruiz-Campos and González-Guzmán 1996). In addition, this taxon has been also categorized as of Special Concern in southern California (Williams et al. 1989; Swift et al. 1993). (2) *Gasterosteus aculeatus microcephalus,* was placed in the category threatened due to its significant population decrease along the northwestern region of Baja California (Ruiz-Campos et al. 1998). That is, of eleven localities where it was historically registered (Smith 1883; Eigenmann 1892; Rutter 1896; Myers 1930; Follett 1960; Miller and Hubbs 1969), it still occurs in only three of them (El Descanso, Santo Domingo and El Rosario streams). And (3) *Oncorhynchus mykiss nelsoni,* whose conservation status was previously determined as stable in the two main drainages of its distribution (San Rafael and Santo Domingo; Ruiz-Campos and Pister 1995).

Several types of anthropogenic disturbances were detected in the aquatic and riparian habitats of the study area (Figures 4a-b). All streams presented some type of disturbance, depending on their nearness to the adjacent urban and agricultural areas. The recreational activities, especially the use of these sites for camping, generate the garbage proliferation that affects the quality of the habitats. These types of disturbance are evident in those streams located between Rosarito and Ensenada, where increased urbanization exists. In addition, the streams situated south of Ensenada are subject to progressive alteration of their aquatic and riparian habitats due to agricultural and livestock practices, which promote siltation.

Recommendations on Conservation and Management

Some recommendations for conservation and management of the native fish fauna and their habitats in the northwestern Baja California, which are derived from the present study, are as follows: (1) strictly prohibit the use and transformation of the estuarine-riverine ecosystems for building of marinas and other tourist facilities, which may cause significant alterations on their hydrological, physicochemical, and biological attributes; (2) prevent the discharge of urban sewage into the streams as well as the use of their riparian ecosystems for depositing garbage; (3) prohibit the deforestation of lands adjacent to streams for expansion of agriculture practices, since it promotes the erosion and siltation of streams' channels; (4) restrict the use of the riparian habitats as grazing sites by livestock as it deteriorates the aquatic habitats and increases the siltation of the streams; (5) periodically monitor the levels of coliform bacteria and pesticides in the coastal streams of the region in order to evaluate the impact by urban pollution and agriculture practices; (6) strictly prevent the introduction of exotic fishes into the aquatic ecosystems of this region, which might harmfully interact with the native fish fauna; and, (7) design a program of holistic conservation at level of basins for the protection of the aquatic and riparian biota.

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Appendix 1. Fish collecting localities in the northwestern region of Baja California, Mexico.

Locality	Coordinates
1.–Bocana Arroyo Cantamar (= Médano), Rosarito.	32° 13′ 44.2″ N, 116° 55′ 21.5″ W
2.–Bocana Arroyo El Descanso (= La Posta), Rosarito.	32° 12′ 09.3″ N, 116° 54′ 47.8″ W
3.–Bocana Arroyo La Misión (= Guadalupe), Ensenada.	32° 05′ 32.0″ N, 116° 52′ 50.0″ W
4.–Arroyo Guadalupe at Rancho Santa Rosa (= El Salto), Ensenada.	32° 13′ 43.9″ N, 116° 55′ 21.6″ W
5.–Arroyo Guadalupe at Rancho Tierra Santa (Ejido El Porvenir), Ensenada.	32° 05′ 00.0″ N, 116° 37′ 00.0″ W
6.–Bocana Arroyo San Miguel (= El Carmen o San Antonio), Ensenada.	31° 54′ 05.8″ N, 116° 43′ 48.4″ W
7.–Arroyo Las Animas at Ejido Uruapan, Ensenada.	31° 37′ 00.0″ N, 116° 26′ 00.0″ W
8.–Bocana Arroyo Santo Tomás, Ensenada.	31° 32′ 12.9″ N, 116° 39′ 28.0″ W
9.–Arroyo Santo Tomás at Ejido Ajusco, Ensenada.	31° 35′ 00.0″ N, 116° 28′ 00.0″ W
10.–Bocana Arroyo San Vicente, Ensenada.	31° 15′ 54.3″ N, 116° 22′ 51.7″ W
11.–Bocana Arroyo El Salado (ca. Loma Linda), Ensenada.	31° 06′ 35.5″ N, 116° 17′ 50.4″ W
12.–Arroyo Seco (tributary of Arroyo San Rafael) ca. Colonet, Ensenada.	31° 05′ 56.1″ N, 116° 10′ 58.9″ W
13.–Bocana Arroyo San Rafael ca. Punta Colonet, Ensenada.	30° 58′ 08.1″ N, 116° 16′ 29.8″ W
14.–Bocana Arroyo San Telmo ca. Punta San Telmo, Ensenada.	30° 56′ 29.5″ N, 116° 14′ 57.6″ W
15.–Bocana Arroyo Santo Domingo ca. San Ramón, Ensenada.	30° 42′ 53.6″ N, 116° 02′ 31.6″ W
16.–Arroyo Santo Domingo at Rancho El Divisadero (ca. Misión), Ensenada.	30° 46′ 21.4″ N, 115° 54′ 19.5″ W
17.–Bocana Arroyo San Simón (ca. Ejido Papalote), Ensenada.	30° 27′ 04.1″ N, 115° 55′ 36.3″ W
18.–Bocana Arroyo San Simón (1 km above Hotel La Pinta), Ensenada.	30° 24′ 24.1″ N, 115° 54′ 24.3″ W
19.–Bocana Arroyo El Rosario, Ensenada.	30° 02′ 32.5″ N, 115° 47′ 15.6″ W
20.–Arroyo Neji ca. Ejido Neji, Tecate.	32° 23′ 00.0″ N, 116° 19′ 00.0″ W
21.–Laguna Hanson, Sierra Juárez, Ensenada.	32° 02′ 00.0″ N, 115° 54′ 00.0″ W
22.–Arroyo San Carlos at Rancho Alamitos (4.3 mi E Highway 1), Ensenada.	31° 46′ 00.0″ N, 116° 31′ 00.0″ W
23.–Arroyo San Rafael at Rancho Mike's Sky, Sierra San Pedro Mártir.	31° 06′ 35.0″ N, 115° 38′ 05.0″ W
24.–Arroyo San Rafael at Rancho Garet, Sierra San Pedro Mártir.	31° 04′ 25.0″ N, 115° 36′ 05.0″ W
25.–Arroyo El Potrero at Rancho El Potrero, Sierra San Pedro Mártir.	30° 55′ 00.0″ N, 115° 38′ 45.0″ W
26.–Arroyo La Grulla at La Grulla meadow, Sierra San Pedro Mártir.	30° 53′ 30.0″ N, 115° 29′ 00.0″ W
27.–Arroyo San Antonio de Murillos at Rancho San Antonio, Sierra San Pedro Mártir.	30° 48′ 45.3″ N, 115° 37′ 47.3″ W
28.–Arroyo La Zanja, Sierra San Pedro Mártir.	30° 49′ 12.0″ N, 115° 37′ 38.0″ W
29.–Arroyo San Antonio ca. confluencia del Arroyo La Zanja, Sierra San Pedro Mártir.	30° 49′ 08.8″ N, 115° 37′ 45.3″ W

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Range Extensions, Taxonomic Notes and Zoogeography of Symbiotic Caridean Shrimp of the Tropical Eastern Pacific (Crustacea: Decapoda: Caridea)

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Abstract.—Range extensions are presented for 14 symbiotic shrimp or obligate invertebrate predators that live with echinoderms, gorgonians, antipatharians or corals. *Tulearocaris holthuisi* Hipeau-Jacquotte, previously reported from the Indo-Pacific region, is reported for the first time from the eastern Pacific. Host records are given for the first time for *Chacella tricornuta* Hendrickx and *Pseudocoutierea elegans* Holthuis. *Harpiliopsis spinigera* (Ortmann) co-occurs with *H. depressa* (Stimpson) in the eastern Pacific. The former has been considered to be a synonym of the latter, but they can be differentiated by morphology and living color. Like the Indo-Pacific region, the tropical eastern Pacific has shrimp that live among corals of the genus *Pocillopora* and on echinoids and starfishes. Unlike the Caribbean and western Atlantic, there are few species that associate with sea anemones, crinoids or sponges. Species of *Chacella* and *Veleronia* are endemic to the eastern Pacific.

Tropical caridean shrimp include many species that associate with other invertebrates. These shrimp tend to have preferred hosts, but may associate with other species if the preferred host is not available. Often, the entire postlarval life cycle is spent on a host (Bruce 1976). Coral-associated shrimp may feed on mucus from the host, and also on small invertebrates, algae and sediment (Patton 1974). *Hymenocera picta* may damage its host to the point of death (Hoover 1998). For purposes of this paper, a shrimp that generally is found on or in close association with another invertebrate or colony is termed symbiotic, regardless of whether the association is harmless, mutually beneficial, parasitic all or part of the time, or predatory. Because of their small size (often less than 20 mm total length) and cryptic habits, the details of the associations of many of these species with their hosts are poorly known. It is difficult to say on the basis of a few records whether a species is an obligate associate, unable to survive away from the host; or a facultative associate, able to survive for some time away from a host but usually found in association with it. Some species are known only from the original description.

During field studies between La Paz and Cape San Lucas, Baja California Sur, Mexico in 1997 and the Galapagos Islands in 1998, several interesting symbiotic shrimp were collected. In addition, specimens were found among the collections of the Los Angeles County Museum of Natural History (LACM), and others were sent to us for identification by biologists at the Charles Darwin Research Station, Santa Cruz Island, Galapagos (CDRS); the Universidad de Baja California Sur, La Paz (UBCS) and the Instituto del Mar del Peru (IMARPE). After examination, the specimens were returned to their respective institutions, except for the specimens from Peru, which were donated to the Los Angeles County Museum of Natural History.

This paper presents range extensions and a first record for species from the eastern Pacific. The term "tropical" is used for species living in marine waters with a temperature of 20° C or more for much of the year, whether or not the area is geographically within the tropics. Records are given for two species previously known only from the original description. General zoogeographic patterns and host associations are discussed.

Examination of specimens of *Harpiliopsis* from the eastern Pacific showed that both *H. depressa* and *H. spinigera* are present. Previous works (Holthuis 1951; Wicksten 1983, 1991) considered *H. spinigera* to be a synonym of *H. depressa.* However, Chace and Bruce (1993) distinguished between the two species. We provide illustrations and comments on morphology and living color to assist in identification of the two species.

First Record from the Eastern Pacific

Family Palaemonidae

Tuleariocaris holthuisi Hipeau-Jacquotte 1965

Previous reported range: Madagascar; Hawaii (Hipeau-Jacquotte 1965; Castro 1971; Hoover 1998).

Material: 1 specimen. Pelican Rock, Cape San Lucas, Baja California Sur, Mexico, 5 m, 26 Jul 1997, L. Hernández and party, UBCS. 1 specimen, Arenas Point, Baja California Sur, 10 m, 30 Jul 1997, L. Hernández and party, UBCS. All of the specimens were found clinging to the spines of the longspined sea urchin *Diadema mexicanum* A. Agassiz.

Remarks: Species of *Tuleariocaris* live on echinoids (Chace and Bruce 1993). The specimens from Baja California agree exactly with the description of the species. The shrimp were colored completely dark purple to black, matching the color of the spines of the sea urchin. See Hoover (1998) for a photograph.

Range Extensions in the Eastern Pacific

Family Alpheidae

Synalpheus charon (Heller 1861)

Previous reported range: Indo-West Pacific from Red Sea to Hawaii, Cerralvo Island, Gulf of California to Malpelo Island, Colombia; Clarion and Clipperton Islands (Castro 1971; Wicksten and Hendrickx 1992; Hoover 1998).

Material: 5 specimens. South entrance, Sullivan Bay, Santiago Island, Galapagos, 6 m, among *Pocillopora* sp., 21 Aug 1998, C. Hickman, Jr. and party, CDRS.

Remarks: This species associates with hermatypic corals of the genus *Pocillopora.* In life, it is colored dark orange-red over all of the dorsal and lateral surfaces.

Family Hippolytidae

Thor amboinensis (de Man 1888)

Previous reported range: Indo-West Pacific from Bay of Bengal to Caroline Islands, Western Atlantic and Caribbean from Florida Keys to Tobago; Cocos Island, Costa Rica; Pearl Islands, Panama (Wicksten and Hendrickx 1992; Chace 1997).

Material: 1 specimen. South entrance, Sullivan Bay, Santiago Island, Galapagos, 6 m, among corals, 21 Aug 1998, C. Hickman, Jr. and party, CDRS. 2 specimens. Mosquera Island, Galapagos, 11 m, among corals, 20 Aug 1998, C. Hickman, Jr. and party; CDRS.

Remarks: *Thor amboinensis* always associates with anthozoans. Specimens from the Indo-Pacific region often are found among hermatypic corals. In the Atlantic and Caribbean, a sea anemone often is the host, especially *Condylactis gigantea* (Weinland). The species is recognizable by its polka-dot coloration of large white lateral spots and saddles against a chocolate-brown background, becoming bluish by night. Patton (1974) noted that specimens in Australia had different color patterns if they inhabited corals rather than sea anemones. In life, the abdomen is held flexed vertically upward.

Family Palaemonidae

Allopontonia iaini Bruce 1972

Previous reported range: Indo-Pacific from Zanzibar to Australia; El Bajo, Baja California Sur, Mexico (Bruce 1987).

Material: 2 specimens. Los Islotes (north of Partida Island), Baja California Sur, Mexico, 26 Feb 1994. 2 specimens, same location, 27 Jun 1994. 1 specimen, same location, 1994 (date not specified). 1 specimen, same location, 16 Oct 1994. 1 specimen, same location, 18 Nov 1994. All collected by L. Hernández, UBCS.

Remarks: This species usually associates with sea urchins. At El Bajo, the host was *Asthenosoma* sp. The host of the latest specimens was not recorded.

Chacella kerstitchi (Wicksten 1983)

Previous reported range: San Carlos and San Pedro Nolasco Islands, Sonora, Gulf of California (Wicksten 1983).

Material: 1 specimen. Punta Sal, 20 km. south of Tumbes, Peru, among gorgonians, 11 Aug 1998, Yuri Hooker, LACM.

Remarks: The species previously was collected on antipatharians, *Antipathes* sp.

Chacella tricornuta Hendrickx 1990

Previous reported range: Tres Marías Islands, Nayarit, Mexico (Hendrickx 1990).

Material: 7 specimens, off Los Islotes, Baja California Sur, Mexico, 27 Jul 1997, 32 m, on antipatharians, C. Sánchez, L. Hernández and party, UBCS.

Remarks: In life, this small shrimp clings to antipatharians (*Antipathes* sp.) The large dorsal spines and overall yellow color mimic the polyps of the host.

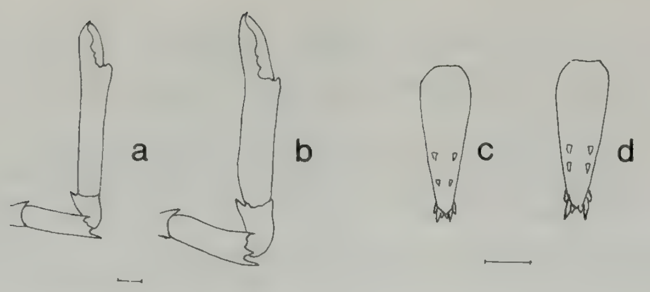

Fig. 1. Right second pereopods and telsons of *Harpiliopsis spinigera* and *H. depressa*. a, *H. spinigera*; b, *H. depressa*; c, *H. spinigera*; d, *H. depressa*. *Harpiliopsis spinigera* from Sullivan Bay, Galapagos; *H. depressa* from Espíritu Santo Island, Mexico. Scale is 1 mm.

Fennera chacei Holthuis 1951

Previous reported range: Indo-West Pacific from western Indian Ocean to Australia and Hawaii; Isabel Island, Mexico to Galapagos (Wicksten and Hendrickx 1992).

Material: 7 specimens, Los Islotes, Baja California Sur, Mexico, among branched coral *Pocillopora elegans* Dana; 23 Jul 1997, L. Hernández. 2 specimens, same location and host, 22 Jan 1995, L. Hernández, UBCS.

Remarks: This species always associates with the corals *Porites* and *Pocillopora* spp. (Holthuis 1951).

Gnathophylloides mineri Schmitt 1933

Previous reported range: Caribbean and western Atlantic, Zanzibar, Seychelles Islands, Hawaii; Malpelo Island, Colombia (Wicksten and Hendrickx 1992).

Material: 1 specimen. Galapagos Islands (no other data), 1997, among spines of sea urchin *Tripneustes depressus* A. Agassiz, CDRS

Remarks: This species usually associates with sea urchins (Bruce 1982). See Hoover (1998) for a photograph.

Harpiliopsis spinigera (Ortmann 1890)

Fig. 1 a, c

Previous reported range: Phillipines; Pearl Islands, Panama (Abele and Patton 1976; Chace and Bruce 1993).

Material: 75 specimens, Calerita, Baja California Sur, Mexico, intertidal, among branched coral, *Pocillopora* sp., 23 Jul 1977, C. Sánchez, L. Hernández and party, UBCS. 4 specimens. San Gabriel Bay, Espíritu Santo Island, Gulf of California, Mexico; shallow area with corals, 20 Feb 1936, *Velero III* sta. 501-36, LACM. 5 specimens. South entrance, Sullivan Bay, Santiago Island, Galapagos, 6 m, among coral, *Pocillopora* sp., 21 Aug 1998, C. Hickman, Jr. and party, CDRS. 2 specimens. South Channel, between Baltra and Santa Cruz Islands, Galapagos, 11 m, among *Pocillopora* sp., 20 Aug 1998, C. Hickman, Jr. and party, CDRS. Also 401 additional specimens from Los Islotes, Baja California Sur, Mexico, 1994-1995, among *Pocillopora elegans*, L. Hernández, UBCS.

Remarks: Species of *Harpiliopsis* live among corals of the genus *Pocillopora*. Holthuis (1951) considered *H. spinigera* and *H. depressus* (Stimpson 1860) to be synonyms. Following Holthuis, Wicksten (1983, 1991) recorded only *H. depressus* from the Gulf of California, southwestern Mexico, Cocos Island and the Galapagos, but noted that *H. spinigera* might be present in the area. Castro (1971) listed *H. spinigera* (as *Anchistia spinigera* Ortmann 1890) as a synonym of *H. depressus.* Chace and Bruce (1993) distinguished between the two species on the basis of the proportions of the chela and merus of the second pereopod and the spacing of the spines of the telson. In their work, the second species is spelled as *H. depressa,* not *H. depressus.* We have provided illustrations to aid in distinguishing between the two species. In *H. spinigera,* the major chela is more slender and the posterior pair of dorsolateral spines of the telson arise about midway between the anterior pair and the posterior end (Fig. 1a, c). In *H. depressa,* the major chela is robust and the posterior pair of dorsolateral spines of the telson arise nearer to the anterior pair than to the posterior end (Fig. 1b, d). Both species occur in the eastern Pacific. We have examined specimens of *H. depressa* from Cerralvo Island, Espíritu Santo Island, and Calerita, Baja California Sur, Mexico from the collections of UCBS and LACM. In life, *H. depressa* tends to be larger than *H. spinigera* and has a color pattern of olive green with a few grayish dorsal stripes, a few white spots and dark band across the tail fan and a dark spot at the base of the movable finger of the major chela. (See Hoover 1998 for a color photograph of *H. depressa* in Hawaii). *Harpiliopsis spinigera* is more slender and has a color pattern of dark green spots on the body with darker pigmentation on the chelipeds and tail fan. *Harpiliopsis spinigera* is much more common than *H. depressa* in the vicinity of La Paz, Espíritu Santo Island and Partida Island, although both species may be found living in the same coral head.

Specimens from Espíritu Santo Island (*Velero III* sta. 501-36, LACM) previously identified as *H. depressus* by Holthuis (1951) are a mixture of *H. depressa* and *H. spinigera.* We have been unable to re-examine all of the specimens mentioned by Holthuis (1952) and Wicksten (1983, 1991) to verify their species designation. Existing specimens should be re-examined or new ones collected to verify which species lives in a particular area.

Hymenocera picta Dana 1852

Previous reported range: Indo-West Pacific from Red Sea and Zanzibar to Hawaii; Taboga Island, Panama; Gorgona Island, Colombia (Wicksten and Hendrickx 1992; Chace and Bruce 1993; Hoover 1998).

Material: 2 specimens. South Channel, between Baltra and Santa Cruz Islands, Galapagos; 8 m, feeding on unidentified starfish, 20 Aug 1998, C. Hickman, Jr. and party, CDRS.

Remarks: This easily recognized shrimp is a predator on starfishes. See Hoover (1998) for a photograph. In addition to the material examined, we have seen clear photographs of this species from El Ocotal, Costa Rica.

Periclimenes soror Nobili 1904

Previous reported range: Indo-West Pacific from Red Sea and Zanzibar to Australia, Marshall Islands and Hawaii; Cholla Bay, Sonora, Gulf of California; Taboga Island, Panama (Bruce 1978; Wicksten and Hendrickx 1992; Hoover 1998).

Material: 3 specimens, Calerita, Baja California Sur, Mexico, intertidal, under *Acanthaster ellisii* (Gray), 23 Jul 1997, C. Sánchez, L. Hernández and party. 2 specimens, on starfish *Mithrodia bradleyi* Verrill; 1 specimen, on starfish *Asteropsis carinifera* (Lamarck); Pelican Rock, Cape San Lucas, Baja California Sur, Mexico; 26 Jul 1997, C. Sánchez. L. Hernández and party, UBCS. 3 specimens, Mosquera Island, Galapagos, 12 m, on starfish *Nidorellia armata* (Gray), 20 Aug 1998, C. Hickman, Jr. and party, CDRS. 2 specimens, Conway Bay, Santa Cruz Island, Galapagos, 5-10 m, on starfish, 22 Aug 1998, C. Hickman, Jr. and party. 1 specimen, Sullivan Bay, Santiago Island, Galapagos, 5 m, 21 Aug 1998, C. Hickman, Jr. and party, CDRS. 1 specimen. Sombrero Chino (near Santiago Island), Galapagos, 10 m, 21 Aug 1998, C. Hickman, Jr. and party, CDRS.

Remarks: All of these shrimp were found on the oral surfaces of starfishes. The color of the shrimp varied with the species of starfish on which they were found. See Hoover (1998) for a photograph.

Pontonides sympathes de Ridder and Holthuis 1979

Previous reported range: Pitt Point, San Cristobal Island; near Daphne Major Island and near Champion Island, Galapagos (de Ridder and Holthuis 1979).

Material: 1 specimen. SW side of Marchena Island, Galapagos, 17-26 m., sand, rock and rubble; 19 May 1984, LACM field party, LACM station G AL84-36.

Remarks: This species associates with antipatharians.

Pseudocoutierea elegans Holthuis 1951

Previous reported range: Santa Catalina Island, California to Galapagos Islands (Wicksten and Hendrickx 1992).

Material: 6 specimens. Sal Point, Peru, among gorgonians. 11 Aug 1998. Yuri Hooker, LACM.

Remarks: At Santa Catalina Island, California, this species lives on the sea whip *Lophogorgia chilensis* (Verrill). The shrimp is colored rose red, like the gorgonian. Field notes suggest that it may occur with other species as well.

Veleronia serratifrons Holthuis 1951

Previous reported range: Off La Libertad, Ecuador; Galapagos Islands (Wicksten and Hendrickx 1992).

Material: 8 specimens. Sal Point, Peru, among gorgonians. 11 Aug 1998. Yuri Hooker, LACM.

Remarks: Specimens of *V. serratifrons* from Kicker Rock, San Cristobal Island, Galapagos have been collected on the gorgonian *Thesea* sp. (Gary Williams, California Academy of Sciences, pers. comm.)

General Comments on Symbiotic Carideans of the Eastern Pacific

Besides the species mentioned in the range extensions, 10 other symbiotic carideans are known from the tropical eastern Pacific. Table 1 presents a list of all symbiotic carideans known from the area. See Wicksten and Hendrickx (1992) for a checklist giving ranges, and Holthuis (1951) for host associations of palaemonids.

Species of *Pontonia* are most widespread of eastern Pacific symbiotic carideans, living in both temperate and tropical areas. Often, a pair lives within the mantle cavity or branchial region of their host, which is a mollusk or ascidian. Because other species of *Pontonia* always associate with invertebrate hosts, it is assumed that *P. longispina* Holthuis and *P. pusilla* Holthuis also are symbiotic, although there is no record of their hosts.

Table 1. Symbiotic Carideans of the Tropical Eastern Pacific.

Species	Hosts and references
Family Alpheidae	
Alpheus lottini Guérin 1829	Corals, *Pocillopora* spp. (Castro 1971, Patton 1974)
Leptalpheus mexicanus Rios and Carvacho 1983	Mud shrimp, *Upogebia* sp. (Ríos and Carvacho 1983, Campos et al. 1995)
Synalpheus charon (Heller 1861)	Corals, *Pocillopora* spp. (Castro 1971)
Family Hippolytidae	
Thor amboinensis (de Man 1888)	Cnidarians (Chace 1997)
Family Palaemonidae	
Allopontonia iaini Bruce 1972	Echinoids (Bruce 1987)
Chacella kerstitchi (Wicksten 1983)	Antipatharians (Wicksten 1983)
Chacella tricornuta Hendrickx 1990	Antipatharians (this paper)
Fennera chacei Holthuis 1951	Corals, *Pocillopora* and *Porites* spp. (Holthuis 1951, Chace and Bruce 1993)
Gnathophylloides mineri Schmitt 1993	Echinoids (Chace and Bruce 1993)
Harpiliopsis depressa (Stimpson 1860)	Corals, *Pocillopora* spp. (Holthuis 1951)
Harpiliopsis spinigera (Ortmann 1890)	Corals, *Pocillopora* spp. (Chace and Bruce 1993)
Hymenocera picta Dana 1852	Asteroids (Hoover 1998)
Periclimenes soror Nobili 1904	Asteroids (Bruce 1978)
Pontonia chimaera Holthuis 1951	Gastropods, *Strombus galeatus* Swainson (Holthuis 1951)
Pontonia longispina Holthuis 1951	Unknown (Holthuis 1951)
Pontonia margarita Smith 1869	Pearl oysters, *Pinctada mazatlanica* (Hanley) and others (Holthuis 1951)
Pontonia pinnae Lockington 1878	Pelecypods, *Pinna rugosa* (Sowerby), *Atrina tuberculosa* (Sowerby), *Laevicardium elatum* (Sowerby) and *Megapitaria aurantiaca* (Sowerby) (Campos 1988, Campos et al. 1992, Campos et al. 1995)
Pontonia pusilla Holthuis 1951	Unknown (Holthuis 1951)
Pontonia simplex Holthuis 1951	Pen shells, *Pinna* sp. (Holthuis 1951)
Pontonia spighti Fujino 1972	Ascidian, *Rhopalaea birkelandi* Tokioka (Fujino 1972)
Pontonides sympathes De Ridder and Holthuis 1979	*Antipathes galapagensis* Deichmann (De Ridder and Holthuis 1979)
Pseudocoutierea elegans Holthuis 1951	Gorgonians, *Lophogorgia chilensis* (this paper)
Tulearocaris holthuisi Hipeau-Jacquotte 1965	Echinoids (Castro 1971, Hoover 1998)
Veleronia laevifrons Holthuis 1951	Gorgonians, *Pacifigorgia* spp. and *Muricea* spp. (De Ridder 1980)
Veleronia serratifrons Holthuis 1951	Gorgonians, *Muricea appressa* Verrill, *Thesea* sp. (De Ridder 1980, this paper)

The species that associate with *Pocillopora* spp. tend to be very widespread, occuring from the western Indian Ocean and Red Sea to the eastern Pacific. Species of *Pocillopora* do not occur in the Caribbean and western Atlantic. The species diversity of coral-associated shrimp is greatest in the tropical Indo-Pacific, where some species of shrimp associate only with particular species of hosts. However, species of *Pocillopora* are difficult to identify to species, especially in the field. See Bruce (1976) for a good review of the specializations of coral-associated shrimp and Chace and Bruce (1993) for keys and general information on palaemonids.

In Panama, coral-associated snapping shrimp (*Alpheus lottini* Guérin-Méneville 1830) and crabs (*Trapezia ferruginea* Latreille 1825) defend their coral from predatory starfishes. Although they feed on coral mucus, the relationship between the crustaceans and the coral seems to be mutualistic; the decapods receive a meal and shelter in return for driving predators away from their coral head (Glynn 1976). *Synalpheus charon* lives in crevices at the bases of coral heads (Castro 1971), but its relationship with the coral and other inhabitants of the colony or its predators is unknown.

The eastern Pacific also contains carideans associated with antipatharians and gorgonians. Of these, species of *Chacella* and *Veleronia* are endemic to the eastern Pacific. Little is known about the natural history of species of *Chacella.* De Ridder (1980) found that, at the Galapagos, *Veleronia laevifrons* lived on three species of *Pacifigorgia* and two species of *Muricea. Veleronia serratifrons* was found only on *Muricea appressa,* but both species could live on a single host. In *V. laevifrons,* the color varied with the host. Further studies on host preferences in these two genera and *Pontonides sympathes* are complicated by taxonomic uncertainties regarding eastern Pacific antipatharian and gorgonian species.

Unlike the Indo-Pacific and Caribbean-western Atlantic regions, the eastern Pacific is relatively poor in species of *Periclimenes.* One of them is associated with starfishes, the other three are free-living. The tropical eastern Pacific does not have an ecological equivalent to the sea anemone commensals *Periclimenes pedersoni* Chace 1958 or *P. yucatanicus* (Ives 1891) of the Caribbean-western Atlantic, or *P. brevicarpalis* (Schenkel 1902) of the western Pacific.

Five eastern Pacific carideans associate with echinoderms or eat them. The diversity of echinoderms is low compared to the Indo-West Pacific, where 50 species of echinoderm symbionts are known (Bruce 1982). Shallow-water crinoids are absent in the tropical eastern Pacific, so crinoid-associated species of *Periclimenes* are missing.

For the most part, large sponges are absent in the tropical eastern Pacific. Such is not the case in the Caribbean-western Atlantic, where large sponges are a prominent feature of reef ecosystems. Eight species of *Synalpheus* may be found solely or primarily within the canals of large sponges (Duffy 1992). Species of *Synalpheus* related to these sponge dwellers have been collected in the eastern Pacific, but without information on their associations. Species of *Typton* and *Periclimenaeus* (family Palaemonidae) also associate with sponges (Holthuis 1951; Ríos 1986). However, the eastern Pacific species have not been studied to determine whether or not they regularly associate with sponges of a particular taxonomic group, or if they are as likely to be found away from a sponge as in one.

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RESEARCH NOTES

Reproduction in the Speckled Rattlesnake, *Crotalus mitchellii* (Serpentes: Viperidae)

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The speckled rattlesnake, *Crotalus mitchellii* (Cope, 1861) occurs from southern Nevada to the tip of Baja California and southern California to northwest and west central Arizona from sea level to around 2440 m (Stebbins 1985). It is one of 6 rattlesnake species to occur in southern California (Stebbins 1985). There are only anecdotal reports on reproduction in this species (Klauber 1936; Cunningham 1959; Brattstrom 1965; Lowe et al. 1986). Klauber (1972) provided information on sizes of egg-sets and broods. The purpose of this paper is to provide information on the seasonal ovarian and testicular cycles of *C. mitchellii* and to provide additional litter sizes.

A sample of 99 specimens of *C. mitchellii* (42 females, Mean Snout-Vent Length, SVL = 673 mm ± 82 SD, range = 520–825 mm); (57 Males, Mean SVL = 708 mm ± 137 SD, range 512–1047 mm) from Arizona, California and Nevada was examined from the herpetology collections of Arizona State University, Tempe, (ASU), the Natural History Museum of Los Angeles County (LACM) and The University of Arizona, Tucson (UAZ) (Appendix). Snakes were collected 1951–1990. Counts were made of enlarged follicles (> 10 mm length). The left testis, vas deferens and part of the left kidney were removed from males; the left ovary was removed from females for histological examination. Tissues were embedded in paraffin and cut into sections at 5 μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; ovary slides were examined for the presence of yolk deposition. Vasa deferentia were examined for sperm. Slides of kidney sexual segments were examined for secretory activity. Because some of the specimens were road-kills, not all tissues were available for histological examination due to damage or autolysis. In road-killed males, the kidneys typically underwent autolysis before the reproductive organs. Number of specimens examined by reproductive tissue were: testis = 57, vas deferens = 38, kidney = 50, ovary = 42.

Testicular histology was similar to that reported by Goldberg and Parker (1975) for the colubrid snakes, *Masticophis taeniatus* and *Pituophis catenifer* (= *P. melanoleucus*) and the viperid snake, *Agkistrodon piscivorus* reported by Johnson et al. (1982). In the regressed testes, seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence, there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes and spermatids were occasionally present. In spermiogenesis, metamorphosing spermatids and mature sperm were present.

Males undergoing spermiogenesis were found April–September; regressed testes were found March-June; testes in recrudescence were found March–August

Table 1. Monthly distribution of conditions in seasonal testicular cycle of *Crotalus mitchellii*. Values shown are the numbers of males exhibiting each of the three conditions.

Month	N	Regressed	Recrudescence	Spermiogenesis
March	3	2	1	0
April	11	4	5	2
May	25	3	11	11
June	9	3	3	3
July	4	0	2	2
August	4	0	1	3
September	1	0	0	1

(Table 1). The smallest spermiogenic male measured 512 mm SVL. This was the smallest male included in the study. Sperm were present in the vasa deferentia of the following males: March 2/2 (100%); April 8/8 (100%); May 15/15 (100%); June 7/8 (88%); July 2/3 (67%); August 1/1 (100%); September 1/1 (100%) suggesting *C. mitchellii* has the capacity to breed March-September. Kidney sexual segments were enlarged and contained secretory granules in 16/17 (94%) of males undergoing spermiogenesis; 11/11 (100%) of males with regressed testes and 14/20 (70%) of males with recrudescent testes. On a monthly basis enlarged sexual segments with secretory granules were found in males in the following proportions: March 3/3 (100%); April 8/9 (89%); May 19/23 (83%); June 6/7 (86%); July 2/3 (67%); August 3/4 (75%); September 1/1 (100%). Mating coincides with hypertrophy of the kidney sexual segment (Saint Girons 1982).

Because of insufficient sample sizes from summer and autumn, it is difficult to compare the testicular cycle of *C. mitchellii* with that of other crotalids. The observation of 44% of May males undergoing spermiogenesis may suggest that spermiogenesis occurs primarily in the spring in *C. mitchellii.* This is in contrast to the western rattlesnake, *Crotalus viridis,* the western diamondback rattlesnake, *Crotalus atrox,* the Mojave rattlesnake, *Crotalus scutulatus* and the tiger rattlesnake, *Crotalus tigris* in which the major period of spermiogenesis occurs in summer-autumn (Aldridge 1979a, Jacob et al. 1987; Goldberg 1999). Since the peak of *C. mitchellii* activity occurs in May-June in southern California (Klauber 1931) collections of summer-autumn samples to describe the testicular cycle would be difficult.

One male (LACM 28018) was found in copulation by G. Ahern near Cabazon on the west slope of the San Jacinto Mountains, Riverside County, California at 1800 hours on 11 June 1964. J. W. Warren (c.f. Brattstrom 1965) found a pair of *C. mitchellii* mating in the afternoon at Afton, San Bernardino County on 18 April 1953. Mating in Arizona occurs in April-May (Lowe et al. 1986). Additional field observations are needed before the period in which mating occurs under natural conditions is known.

During the months of female reproductive activity (April–June) (Table 2) 15/34 (44%) *C. mitchellii* showed evidence of reproductive activity (early yolk deposition, enlarged follicles or oviductal eggs). This is slightly higher than the value (35%) reported for *C. tigris* females (Goldberg 1999).

Females with enlarged follicles (> 10 mm length) were found April-June (Table 2). Females in early yolk deposition (i.e., secondary vitellogenesis *sensu* Aldridge

Table 2. Monthly distribution of conditions in seasonal ovarian cycle of *Crotalus mitchellii*. Values shown are the number of females exhibiting each of the three conditions.

Month	N	Inactive	Early yolk deposition	Enlarged follicles (> 10 mm length) or oviductal eggs
March	1	1	0	0
April	12	8	3	1
May	14	8	2	4[1]
June	8	3	0	5
July	1	1	0	0
August	3	3	0	0
September	2	2	0	0
November	1	1	0	0

[1] Only 1 follicle (17 mm length) measured from damaged ovary.

1979b) were found in April–May. The "small eggs" reported 10 June in a female *C. mitchellii* by Cunningham (1959) were likely undergoing early yolk deposition. The smallest reproductively active female (follicles > 10 mm length) measured 552 mm SVL. Mean litter size for 9 females from Table 3 was 5.78 ± 1.79 SD (3–8 range). This value is close to the mean litter size 5.77 ± 2.47 SD (1–10 range) calculated for 22 *C. mitchellii* listed in Klauber (1972). According to Fitch (1985) *C. mitchellii* litter sizes are largest in the north and decrease in southern (Mexican) populations.

Crotalus mitchellii appears to follow a biennial reproductive cycle in which yolk deposition (secondary vitellogenesis *sensu* Aldridge 1979b) commences in summer followed by ovulation the next year which is similar to that reported in other North American rattlesnakes (see Goldberg, 1999). However, *Crotalus atrox* females are believed to bear litters each year in Oklahoma (Fitch and Pisani 1993) as do southern populations of the western rattlesnakes, *Crotalus viridis* (c.f. Fitch 1985). Furthermore, there are reports of different populations of the timber rattlesnake, *Crotalus horridus* following biennial, triennial or quadrennial reproductive cycles (Ernst 1992). Additional reproductive data on *C. mitchellii* from different parts of its range will be needed before the timing of the female reproductive cycle can be ascertained for this species.

Table 3. Litter sizes for *Crotalus mitchellii*.

Date	SVL (mm)	Litter size	Locality	Source
28 April	762	7	Riverside Co., CA	LACM 104878
7 May	552	3	San Bernardino Co., CA	LACM 19894
28 May	760	8	Riverside Co., CA	LACM 104866
10 June	763	7	San Bernardino Co., CA	LACM 19981
14 June	652	4	Riverside Co., CA	LACM 134441
15 June	762	5	San Bernardino Co., CA	LACM 104938
23 June	683	7	Riverside Co., CA	LACM 104926
3 Sept.	634	7[1]	Maricopa Co., AZ	UAZ 43945
16 Sept.	656	4[2]	Maricopa Co., AZ	UAZ 44316

[1] Gave birth to 5 live young and 2 still born in captivity on 3 September.
[2] Gave birth to 4 live young in captivity on 16 September.

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Appendix: Specimens of *C. mitchellii* examined from the herpetology collections of Arizona State University, Tempe (ASU), Natural History Museum of Los Angeles County, (LACM) and The University of Arizona, Tucson (UAZ).

ARIZONA: LA PAZ COUNTY, LACM 107219; UAZ 50218. MARICOPA COUNTY, ASU 1606, 3200, 3583, 3585, 9073, 24342. LACM 112475. UAZ 27594, 42974–42976, 43945, 44316, 49264 YUMA COUNTY, ASU 15834-15836; UAZ 27589, 35672, 35710, 35816, 43976.

CALIFORNIA: INYO COUNTY, LACM 36696, 104871. KERN COUNTY, LACM 134440; UAZ 35814, 35996, 35997. ORANGE COUNTY, LACM 104872–104874 SAN BERNARDINO COUNTY, LACM 19981, 19894, 63974, 104935–104939, 104941, 104945, 104946, 104949, 104951, 104954, 104955, 134443, 138218; UAZ 35813. RIVERSIDE COUNTY, LACM 28018, 52592, 104866, 104878, 104879, 104881–104883, 104885, 104887, 104890, 104892, 104894, 104895, 104898, 104899, 104901–104903, 104905–104909, 104911, 104913, 104915–104917, 104919, 104921–104923, 104925, 104926, 104928, 104929, 134441, 134442, 138217, 19996–19998 SAN DIEGO COUNTY, LACM 52593, 52594.

NEVADA: CLARK COUNTY, UAZ 27597. NYE COUNTY, LACM 134038, 134039.

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Research notes

Reproduction in the Glossy Snake, *Arizona elegans* (Serpentes: Colubridae) from California

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The glossy snake, *Arizona elegans* Kennicott 1859 is a wide-ranging species that occurs in the southwestern United States from southwestern Nebraska and east Texas to central California, southern Utah to southern Baja California, southern Sinaloa and San Luis Potosí, México from below sea level to 1830 m; it inhabits desert, sagebrush flats, grassland, chaparral and woodland (Stebbins 1985). Aldridge (1979a; 1979b) reported on reproduction in *A. elegans* in New Mexico. There are other anecdotal reports on reproduction in *A. elegans* by Burt and Hoyle (1934); Reynolds (1943); Cowles and Bogert (1944); Wright and Wright (1957); Tennant (1984); Degenhardt et al. (1996). Fitch (1970) summarized information on reproduction in *A. elegans.* Biology of the snake genus *Arizona* is summarized in Dixon and Fleet (1976). It is of interest to compare reproduction in populations from different areas of the geographic range of snakes to determine variation in the reproductive cycle. The purpose of this note is to present the first detailed information on the ovarian and testicular cycles of *A. elegans* from California and to provide information on clutch sizes. Reproduction of the California population of *A. elegans* is compared with reproduction of a population of *A. elegans* from New Mexico (Aldridge 1979a; 1979b).

A sample of 111 specimens of *A. elegans* (31 females, mean Snout-Vent Length, SVL = 723.2 mm ± 96.2 SD, range = 562–918 mm); 80 males, mean SVL = 610.3 mm ± 118.2 SD, range = 367–958 mm) from California was examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM) (Appendix). Snakes were collected in 1937–1977. Counts were made of enlarged follicles (> 10 mm length) or oviductal eggs. The left testis, vas deferens and part of the left kidney were removed from males; the left ovary was removed from females for histological examination.

Tissues were embedded in paraffin and cut into sections at 5 μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; ovary slides were examined for the presence of yolk deposition (i.e., secondary vitellogenesis *sensu* Aldridge 1979a). Vasa deferentia were examined for sperm. Slides of kidneys were examined for secretory activity in the sexual segments. Because some of the specimens were road-kills, not all tissues were available for histological examination due to damage or autolysis. Number of specimens examined by reproductive tissue were: testis = 80, vas deferens = 55, kidney = 38, ovary = 31.

Testicular histology was similar to that reported by Goldberg and Parker (1975) for the colubrid snakes, *Masticophis taeniatus* and *Pituophis catenifer* (= *P. melanoleucus*). In the regressed testes, seminiferous tubules contained spermatogonia

Table 1. Monthly distribution of conditions in seasonal testicular cycle of *Arizona elegans* from California. Values shown are the numbers of males exhibiting each of the three conditions.

Month	N	Regressed	Recrudescence	Spermiogenesis
April	11	10	1	0
May	50	46	4	0
June	14	10	3	1
July	4	0	3	1
September	1	0	0	1

and Sertoli cells. In recrudescence, there was renewal of spermatogenic cells characterized by spermatogonial divisions. Primary and secondary spermatocytes and spermatids were occasionally present. In spermiogenesis, metamorphosing spermatids and mature sperm were present.

In the spring (April–June), 66/75 (88%) of males contained regressed testes (Table 1). Testes in 11/80 (14%) were undergoing recrudescence. Spermiogenesis was occurring in the following males: 1/14 (7%) June; 1/4 (25%) July; 1/1 (100%) September. Vasa deferentia in 55/55 (100%) *A. elegans* males collected in the spring contained sperm (5/5 April; 42/42 May; 8/8 June) suggesting that mating occurs during this period. Ball (1990) reported *A. elegans* males and females collected 13 and 16 May in Oklahoma courted and mated when placed in captivity. The only September male (which was undergoing spermiogenesis) contained sperm in the vas deferens. It is not known whether *A. elegans* mates during autumn. The *A. elegans* testicular cycle appears to fit the "aestival spermatogenesis D" as described by Saint Girons (1982) (spermatogenesis from June to October; ovulation in the beginning of June). Kidney sexual segments of males: 2/2 (100%) April; 27/28 (96%) May; 7/7 (100%) June; 1/1 (100%) September were enlarged and contained secretory granules. Mating coincides with hypertrophy of the kidney sexual segment (Saint Girons 1982).

There were no *A. elegans* males collected in August and only one from September (Table 1). This is a reflection of the seasonal activity cycle of *A. elegans* in southern California in which this species is mainly active during the spring. Of 34 reports of *A. elegans* in San Diego County (Klauber 1931), 28 (82%) were from winter-spring; only 6/34 (18%) were from August–September. The smallest mature male (sperm in the vas deferens, LACM 102083) measured 367 mm SVL. Males smaller than this size were excluded from the study to avoid including immature males in analysis of the testicular cycle.

The timing of the testicular cycle of *A. elegans* in California is similar to that of *A. elegans* in New Mexico (Aldridge 1979b) and *M. taeniatus* and *P. catenifer* (Goldberg and Parker 1975) in which testes are regressed in spring with spermiogenesis occurring later in the year. However, the *A. elegans* testicular cycle is distinctly different from that of the sympatric western shovelnose snake, *Chionactis occipitalis,* which also has a spring activity period in California during which time spermiogensis occurs (Goldberg 1997).

Arizona elegans females with enlarged follicles (> 10 mm length) or oviductal eggs were found May–June (Table 2). One May female was undergoing yolk deposition (= secondary vitellogenesis *sensu* Aldridge 1979a). One June female

Table 2. Monthly distribution of conditions in seasonal ovarian cycle of *Arizona elegans* from California. Values shown are the number of females exhibiting each of the three conditions.

Month	N	Inactive	Yolk deposition	Enlarged follicles (> 10 mm length) or oviductal eggs
March	1	1	0	0
April	4	4	0	0
May	11	5	1	5
June	7	4*	0	3
July	4	4	0	0
August	3	3	0	0
September	1	1	0	0

* Corpora lutea present in one female; eggs had been recently deposited.

(LACM 102023) collected 16 June contained corpora lutea but no oviductal eggs indicating a recent ovulation. Aldridge (1979a) reported *A. elegans* females from New Mexico to also ovulate in June. The smallest reproductively active *A. elegans* female (follicles > 10 mm length, LACM 122093) measured 562 mm SVL. Females smaller than this size were excluded from the study to avoid including immature females in analysis of the ovarian cycle.

Mean clutch size for 8 females with enlarged follicles (> 10 mm length) or oviductal eggs was 7.5 ± 3.2 SD, range = 2–11 (Table 3). This value may be slightly higher than what actually occurs since clutch sizes for 7 of the 8 females (Table 3) came from counts of follicles > 10 mm length. There is a chance that not all enlarged follicles would have completed development. There was no evidence (yolk deposition in progress in a female with oviductal eggs) to suggest females produce more than one clutch per year. Fourteen *A. elegans* clutches from the literature (Fitch 1970) from different locations averaged 8.5, range = 3–23. Aldridge (1979a) reported potential fecundity (enlarged follicles or oviductal eggs) of 8.4 ± 0.7 SE, range 6–12 for 6 *A. elegans* from New Mexico. There was no significant difference between the clutches of Aldridge (1979a) for *A. elegans* from New Mexico and clutches from California *A. elegans* presented herein ($t = 0.925$, $p > 0.30$). Comparisons of larger numbers of clutches will be

Table 3. Clutch sizes for *Arizona elegans* from California estimated from counts of yolked follicles > 10 mm length or oviductal eggs.

Date	SVL (mm)	Clutch size	County	LACM #
4 May	918	11	Riverside	102034
11 May	562	2	Riverside	122093
20 May	897	8	San Diego	52460
24 May	745	9	Riverside	102109
11 June	823	5*	San Diego	102137
15 June	745	9	Riverside	102026
16 June	784	11	Riverside	102027
18 June	699	2	San Bernardino	102124

* Oviductal eggs; other clutches are enlarged follicles.

needed to ascertain differences in fecundity between New Mexico and California populations of *A. elegans.*

Only 9/23 (39%) snakes were reproductively active (enlarged follicles > 10 mm length or oviductal eggs) during March–June. This is within the range of 7–70% found for annual percentages of breeding females per year in their survey of 85 snake species (Seigel and Ford 1987).

In conclusions, the reproductive cycle of *A. elegans* from California appears similar to that of *A. elegans* from New Mexico, ca. 870 km apart (Aldridge 1979a, 1979b) as testes are regressed in both populations in spring; spermiogenesis occurs in late summer. Yolk deposition began in spring in California and New Mexico *A. elegans* with ovulation in June. Additional reproductive studies between widely separated populations of *A. elegans* will be required to ascertain the amount of geographic variation in reproduction in this widely distributed species.

I thank Robert L. Bezy (Natural History Museum of Los Angeles County) for permission to examine *A. elegans.* Michelle Zamora assisted with histology.

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Appendix

Specimens of *A. elegans* from California examined from the herpetology collection of the Natural History Museum of Los Angeles County, (LACM).

IMPERIAL COUNTY, LACM 2178. KERN COUNTY, LACM 101994, 101995, 123758. LOS ANGELES COUNTY, LACM 20392, 20395, 20396, 74056, 74057, 126187, 126190. RIVERSIDE COUNTY, LACM 20436, 52461–52463, 52467, 52468, 52470, 52472, 101993, 102000, 102001, 102003, 102010, 102021–102023, 102026, 102027, 102030, 102032, 102034–102036, 102038, 102040, 102043, 102044, 102046, 102049, 102050, 102054, 102056, 102057, 102062, 102065, 102067–102069, 102072, 102083, 102084, 102086–102088, 102091, 102099, 102101, 102103, 102104, 102106, 102109, 102110, 115764, 122093–122096. SAN BERNARDINO COUNTY, LACM 20440–20444, 20447, 68831, 68832, 102112, 102114, 102115, 102117, 102119–102122, 102124, 102126, 102127, 102130, 102133, 122455, 125989, 138134. SAN DIEGO COUNTY, LACM 27675, 27676, 27678, 27680, 52460, 59071, 66929, 76285, 102136, 102137, 102140, 102146, 102153, 102154, 102156, 102164, 102165, 123756, 126291.

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99(2), 2000, pp. 110–113

New occurrences of the endemic labrisomid fish *Paraclinus walkeri* Hubbs, 1952 in Bahía de San Quintin, Baja California, México.

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Baja California, México.

Paraclinus walkeri (family Labrisomidae) is a small, cryptic species that, since their first collections in 1949 (Hubbs 1952, Rosenblatt and Parr 1969) has been reported only from Bahía de San Quintín, Baja California (México).

A total number of eleven individuals of the *Paraclinus walkeri,* were collected from January to December 1994 in Bahía de San Quintín, as a part of a larger study of the fishes of nearshore environments that included Bahía de Todos Santos, Estero de Punta Banda, and the Bahía de San Quintín and its adjacent coastal waters (Rosales-Casián 1997b).

The Bahía de San Quintín (30°24′–30°30′ N, 115°57′–116°01′ W) is located 300 km south of California border, and is one of the most important lagoons in Baja California (Ibarra-Obando 1990); it has a total area of 4,000 ha, communicates with the sea through a narrow mouth (<1000 m) that is 2–7 m depth, and is divided into two arms: the western arm is called Bahía Falsa and the eastern, Bahía de San Quintín (Fig. 1). The channel bottoms are muddy with fine sediment towards the head, and coarser sand near the mouth (Gorsline and Steward 1962). This bay is classified as an antiestuary, with salinity and temperature values that increase from the mouth towards the head (Chavez-de-Nishikawa and Alvarez-Borrego 1974). It is a protected habitat characterized as a high productivity zone due to the presence of seagrass beds of *Zostera* and *Spartina* (Ballesteros-Grijalva and García-Lepe 1993; Poumian-Tapia 1995), and phytoplankton. In San Quintín, an almost permanent upwelling has been reported close to the mouth (Dawson 1951), and the most intense period was observed during the months of April and May (Rosales-Casián 1997b).

A report by Hubbs (1952) mentioned that the species *P. walkeri* was found only in San Quintín Bay, Baja California, and that it is probably found nearer to the head of the bay than to the mouth. Under natural conditions, the fish live in sponges found on sand bottom, and they were collected from these same sponges which were attached to the pilings of an old pier that Hubbs (1952) assumed to be optimal for this species. The name *walkeri* is attributed to Boyd W. Walker, and the first individual was collected on an expedition of the Stanford Natural History Club on March 24, 1949, from a mud flat. The genus *Paraclinus* (Perciformes: Labrisomidae) currently contains 19 species of which eleven are found in the eastern Pacific (Eschmeyer 1998; Rosemblatt and Parr 1969).

In Bahía de San Quintín, the first published check-list of the fish species reported 69 species belonging to 56 genera and 34 families, including the species *P. integripinis* and *P. walkeri* (Rosales-Casián 1996). The geographic range of *P. integripinis* is from Bahía Almejas, Baja California, México to Santa Cruz Island,

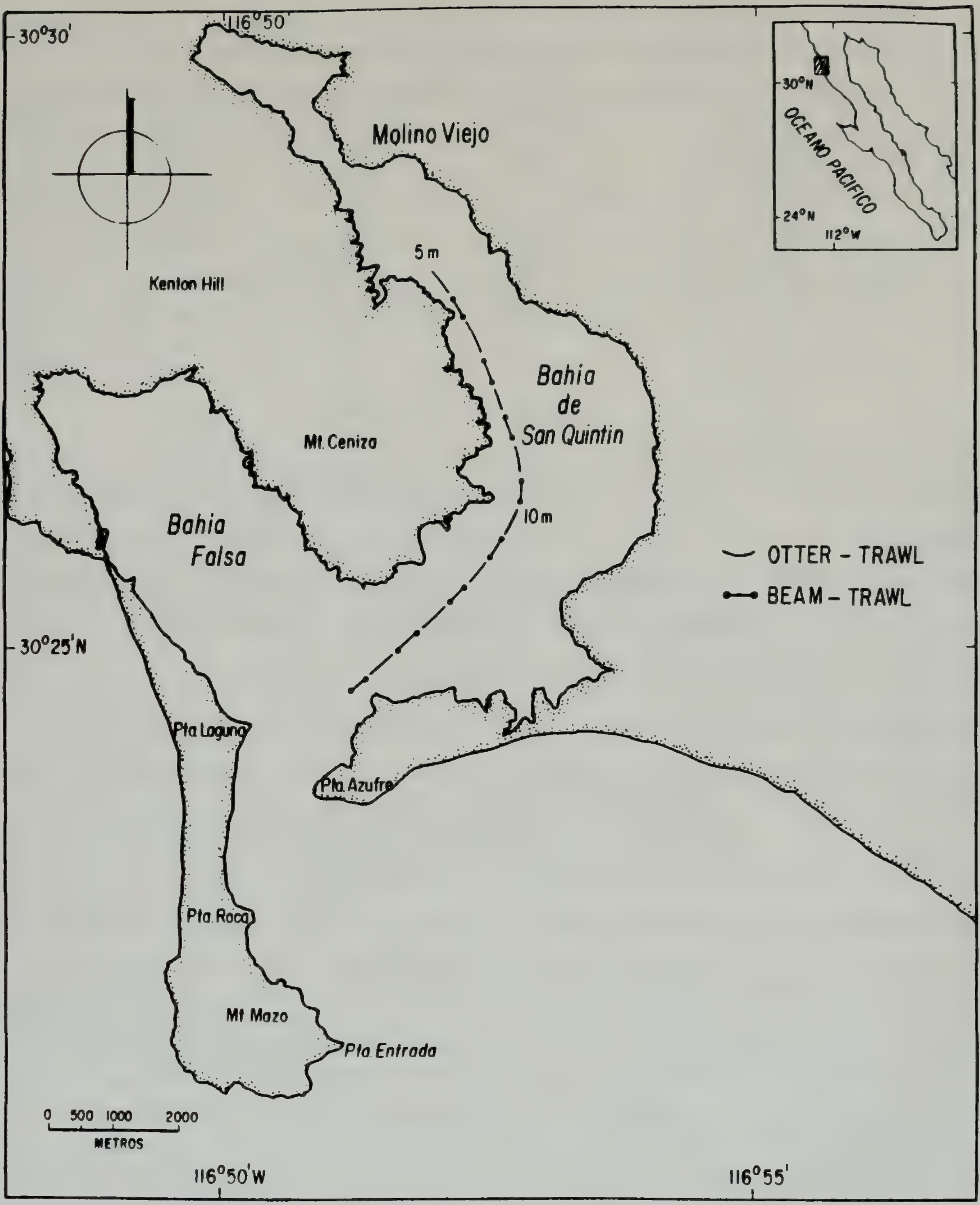
30°30'
116°50'
Molino Viejo
30°N
OCEANO PACIFICO
24°N
112°W
5 m
Kenton Hill
Bahia
de
San Quintin
Mt.Ceniza
10m
Bahia
Falsa
OTTER - TRAWL
BEAM - TRAWL
30°25'N
Pta Laguna
Pta. Azufre
Pta. Roca
Mt Mazo
Pta Entrada
0 500 1000 2000
METROS
116°50'W
116°55'

Figure 1. Location of the sampling sites in Bahía de San Quintín, B.C. México.

California (Miller and Lea 1972). A comparison of the collected fishes with a beam-trawl gear from the Estero de Punta Banda and Bahía de San Quintín is presented in Rosales-Casián (1997a). In this last study, the most important fish species in Punta Banda (5m-depth) were the California halibut (*Paralichthys californicus*), the kelp bass (*Paralabrax clathratus*), and the barred sand bass (*P. nebulifer*); in San Quintín the catches were dominated by the bay pipefish (*Syngnathus leptorhynchus*), *P. californicus*, and the California tonguefish (*Symphurus atricauda*).

In Bahía de San Quintín, the labrisomid *P. walkeri* was collected with two of the five gears during monthly sampling in 1994. These were beam-trawl (1.6 m × 0.4 m, 3-mm mesh), and an otter-trawl (opening of 7.5 m headrope, with 19 mm of body mesh, and 6 mm mesh cod-end), both towed at a velocity of 1.5 knots for five minutes. The beam-trawl collected six individuals at a depth of 5m,

Table 1. Data of *Paraclinus walkeri* collected in Bahía de San Quintín, B.C., México. Collections were made in 1964. TL: Total length, ST: Standard length, W: Total weight.

Month	Gear	Depth (m)	TL (mm)	ST (mm)	W (g)
September	Otter-trawl	10	87	75	7.0
September	Beam-trawl	10	87	73	8.1
September	Beam-trawl	10	82	69	7.1
September	Beam-trawl	10	86	73	9.8
October	Beam-trawl	5	45	39	0.9
October	Beam-trawl	5	45	39	1.1
October	Beam-trawl	5	46	39	1.1
October	Beam-trawl	5	40	35	0.7
October	Beam-trawl	5	47	40	1.3
November	Beam-trawl	5	57	50	2.2
November	Otter-trawl	5	46	38	3.6

and three individuals at a depth of 10m. Two more specimens were collected by otter-trawl, one individual at a depth of 5 and 10m. The collection of specimens occurred from August (n = 1), September (n = 3), October (n = 5), to November (n = 2). The specimens from 5m were captured on the muddy bottom in the channel and were associated with seagrasses (*Z. marina*). *P. walkeri* from 10 m were associated with remains of the same eelgrass during fall (August-November). The collection sites in Bahía de San Quintín are presented in Fig. 1.

Paraclinus walkeri in almost all features of external morphology fits the diagnosis of *P. integripinnis.* The diagnosis is based upon an increase in the number of branchiostegal rays that is 7, rarely 6; body usually with a uniform brown coloration and with 5-7 darker bars; opercular spine with an acute tipe, rarely with two points (Hubbs 1952; Rosenblatt and Parr 1969). For *P. integripinis* a diagnosis is six branchiostegals rays, rarely five and never seven; opercular spine is sharp to blunt or rounded, and may bear as many as three points; the color pattern does not include a barred phase (Rosenblatt and Parr 1969).

The sampling of the 1994 study was not directed to the pier pillings or the sponges that are the habitats for this labrisomid, thus my data cannot be used to estimate population size in Bahía de San Quintín. Its relative abundance from the total fish community (10,079 individuals) in the bay during 1994 was less than 0.11%. In the same period, a total number of 22 specimens of *P. integripinnis* was collected with same gears and depths. The total and standard length and the weight of the collected *P. walkeri* are shown in Table 1; the range of total length was 40 to 87 mm, and the range of the total weight was 0.7 to 9.8 grams.

Paraclinus walkeri seems to behave as a good biological species that is ripe for further research. However it is difficult to conceive how this tiny population, restricted to a small bay and embedded in the range of another very similar species, is able to maintain its genetic integrity (Rosenblatt and Parr 1969).

Nevertheless, it does appear that *P. walkeri* may indeed be restricted to one, relatively small, coastal lagoon because in a similar system, Estero de Punta Banda, it was not collected. How might this species maintain itself and be unable to disperse from that point? First, *P. walkeri* is a very small species, apparently evolved to take advantage of lagoon environments. These systems are quite rare along the Baja California coast and dispersal from these isolated environments may be difficult if a species cannot live along the open coast. Moreover, larval dispersal from Bahía de San Quintín may also be difficult. In a study of DNA of seven populations of an economically important serranid, the kelp bass (*Paralabrax clathratus*), from Baja California (México) and California (USA), Grothues (1994) found that the San Quintín population is an isolated one. Grothues speculated that San Quintín lies in an area of upwelling, and that this may act as a barrier to larval drift, causing larvae moving along shore to be entrained seaward. This coastal lagoon remains as an almost pristine place and makes a special environment for study and comparison with other highly impacted sites from the California coast.

Acknowledgements

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An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, literature cited, tables, figure legend page, and figures. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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Marine Ecology of Rocky Reefs and Areas of Special Biological Significance
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The Puente-Chino Hills Wildlife Corridor and Wildlife Corridors in the Los Angeles Basin.
Organizers: Dan Guthrie (*dguthrie@jsd.claremont.edu*) and Dan Cooper (*dcooper1@pacbell.net*)

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Organizer: Carlos Robles, CSU Los Angeles. (323) 343 2067 *crobles@calstatela.edu*

Dealing with Contaminated Runoff
Organizer: John Dorsey, City of Los Angeles, Stormwater Management Division (213) 847 6347 *jdorsey@san.lacity.org*

There will be additional sessions of Invited Papers and Posters and of papers by Junior Academy members.

Student Awards: Students who elect to participate are eligible for best paper or poster awards in the following categories. Biology: ecology and evolution, biology: genetics and physiology, physical science. A paper by any combination of student and professional co-authors will be considered eligible provided that it represents work done principally by student(s). In the case of an award to a co-authored paper, the monetary award and a one year student membership to the Academy will be made to the first author only.

For further information on posters, abstracts, registration and deadlines, see the Southern California Academy of Science web page at: www.lam.mus.ca.us/~scas/

Student Award Winners

The Annual Meeting of the Southern California Academy of Sciences was held May 19–20 at the University of Southern California. Student award winners were as follows.

Best Poster in Ecology/Evolution

Kelly M. O'Reilly, Dept. of Biological Science, California State University, Fullerton
Meristic and Morphological Variation among California Populations of the Marine Silverside Fish *Atherinops affinis* (Teleostei: Atherinopsidae)

Best Oral Presentation in Ecology/Evolution

Matthew Edwards, Dept. of Biology, University of California, Santa Cruz
El Nino 1997–98: Large-scale Patterns of Disturbance and Recovery in Giant Kelp Forests

Best Poster in Physiology/Genetics

Gerald Lopez, Dept. of Biological Science, California State University, Fullerton
High Creatine Phosphokinase Activity in the White Muscle of the Endothermic Mako Shark

Best Paper in Physiology/Genetics

Jennifer Jarrell, Dept. of Marine Science, University of South Florida
Use of a Synthetic Polypeptide to Determine the Sex and Reproductive Status of Field-caught Red Grouper, *Epinephelus morio*

American Institute of Fisheries Research Biologists; Best Oral Presentation

Darryl Smith, Dept. of Biological Science, California State University, Fullerton
Trophic Position of Southern California Estuarine and Island Populations of the Silverside Fish *Atherinops affinis* (Teleostei: Atherinopsidae): Analyses of 15N and 13C Stable Isotopes and Dietary Items

American Institute of Fisheries Research Biologists; Best Poster

Kristina Louie, Dept of Organismic Biology, Ecology and Evolution, UCLA
Genetic Variation of the Eastern Pacific Bay Pipefish, *Syngnathus leptorhynchus* (Gasterosteiformes: Syngnathidae)

Research Training Program

Based on their oral presentation at the Annual Meeting and the written paper on their research, the following students will attend the National Associated Academy of Sciences meeting, held in conjunction with the American Association of Sciences Meeting in San Francisco in February, 2001.

Heath Gibson, Troy High School
Analysis of a Newly Identified Variable Star in Aquarius

Christel Miller, Calif. Acad. of Math. and Science and Division of Endocrinology, Harbor, UCLA Medical Center Research and Education Institute
Localization and Confirmation of Glycogen Synthase Kinase-3 Beta in the Mouse Testes by Immunohistochemistry

Natalie Sanchez Biological Science, California State Univ. Fullerton
Position of Red Myotomal Muscle in Tunas and Sharks

Ying Jiang Arcadia High School and Dept. of Pathology, USC School of Medicine
Feathered Scales in Silkie Chickens: a Molecular Study

Ronald Solarzano, Alhambra High School: Norris Cancer Center, U.S.C.
Association of Alcohol Dehydrogenase Genotype with Risk of Colon Cancer in Humans

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On the Wildlife of Wetlands of the Mexican Portion of the Rio Colorado Delta

E. Mellink and V. Ferreira-Bartrina

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Abstract.—The delta of the Colorado River, praised for its wealth of wildlife, has been dramatically altered by agriculture. In this article we provide a basic overview of the status of the aquatic wildlife of this area. Overall there is a great lack of knowledge on the status of the different aquatic species in the area, but negative impacts include the disappearance of the massive riparian forests, a reduction in the populations of native fish (very severe), a number of birds, two mammals, and possibly one amphibian and two reptiles. Conversely, habitat transformation might have benefited some amphibians, some birds, and one mammal. Alien aquatic taxa that have been introduced to the area or have colonized it include some plants, 4 invertebrates, more than 20 fish species, 3 amphibians, 3 reptiles, and 1 bird. We conclude that the area is far from being biologically intact, and that it does not meet the legal criteria for being a Biosphere Reserve, as it has been declared. Listing of some of the species as at risk is unsupported. Although the area is biologically very modified, it can provide important opportunities for the conservation of wetland taxa.

Resumen.—El delta del río Colorado, afamado por la riqueza de su fauna silvestre ha sido dramáticamente alterado por la agricultura. En este artículo presentamos ona revisión básica del estado de la fauna acuática en esta área. En general existe un gran desconocimiento del status de las diferentes especies acuáticas, pero los impactos negativos incluyen la desaparición de los bosques riparios masivos, una reducción en las poblaciones de peces nativos (bastante severa), de algunas aves, dos mamíferos y, posiblemente, un anfibio y dos reptiles. Por lo contrario, la transformación del habitat ha beneficiado a algunos anfibios, algunos reptiles y un mamífero. Especies exógenas que se han introducido al área, o que la han colonizado, incluyen algunas plantas, 4 invertebrados, mas de 20 especies de pecas, 3 anfibios, 3 reptiles y 1 ave. Concluímos que el área está lejos de ser biológicamente intacta y que no reune los criterios para ser una reserva de la Biósfera, como ha sido declarada. El listado de algunas de las especies como en riesgo carece de sustento. Aunque el área se encuentra biológicamente muy modificada puede proveer oportunidades importantes para la conservación de taxa acuaticos.

During the early 20th century, sportsman and scientists praised the delta of the Rio Colorado for its wealth of wildlife (Leopold 1949, 1953; Murphy 1917). Earlier, the area had been an attraction for beaver trappers (Mearns 1907; Pattie 1831; Sykes 1937a). However, the biological integrity of the area was dramaticaly altered when agriculture was established at the turn of the century, first in the

United States' Imperial Valley, and, shortly thereafter, in Mexico's Valle de Mexicali. This area has become one of Mexico's prime agricultural areas (Sanchez-Ramirez 1990). This conversion resulted in "the lower Rio Colorado . . . [having] . . . one of the most highly modified channels in western North America. The most characteristic feature of aquatic habitats in arid zones, extreme variability in time and space, has been surpressed . . ." (Minckley 1982).

In this rendering of the river, the extent of wetland habitats has been greatly reduced. Only a few wetland areas remain, including those associated with the Rio Hardy, the Cienega de Santa Clara and the Cienega del Doctor (Glenn *et al.* 1996). The Cienega del Rio Hardy was a large wetland fed by water from the Hardy and the Colorado. The large water discharge of the mid-1980s eroded the natural dam that created it and lead to its draining (J.M. Payne, pers. comm.).

The Cienega de Santa Clara, the largest wetland in the Mexican portion of the delta, is fed mainly by brackish agricultural drain water from Arizona, U.S.A. (Glenn *et al.* 1992, 1996; Zengel *et al.* 1995). Its vulnerability was evidenced by an 8-month interruption in water flow, due to channel repair (Zengel *et al.* 1995). Moreover, if the Yuma Desalting Plant, in southern Arizona, becomes operational it will have very deleterious effects on the emergent vegetation of this wetland (Glenn *et al.* 1992, 1996; Zengel *et al.* 1995).

The Cienega del Doctor owes its existence to the artesian springs along the Cerro Prieto fault, to the east of the delta, which have high plant richness (Ezcurra *et al.* 1988; Zengel *et al.* 1995). Other wetlands in the area include irrigation canals and agricultural drainages, and ephemeral wetlands produced by irrigation water spillover and tailwaters.

On the other hand, fishing activities in the Upper Gulf of California allegedly caused the reduction of totoaba (*Totoaba macdonaldi*), an endemic large sea bass, and vaquita (*Phocoena sinus*), an endemic porpoise. These reductions, and the importance of the area as a shrimp hatchery, have promoted several management and conservation actions by the Mexican government, including *designation* of the delta's marine part as well as the Cienega de Santa Clara as a Biosphere Reserve, in 1993. This category requires that the area be, to a large extent, well preserved. Also, several wildlife species that occur or previously occurred in the area have been listed by the Mexican Federal Government as endangered or threatened.

However, both the species that have been listed and the biological characteristics of the area included in the Biosphere Reserve have remained largely unstudied. It is our intention in this paper to provide a basic overview of the wildlife components of the wetlands of the Mexican portion of the Rio Colorado delta. We do not restrict this review to the area included in the Biosphere Reserve, but refer to the total Mexican portion of the delta.

A cautionary note: the descriptions of the early 20th century are often used as a model of the pristine conditions of this area. However, the large amounts of sediments recorded in the river by Sykes (1937b) reflected a major anomaly. Intensive trapping of beavers along the Colorado and its tributaries in the 19th century promoted an increase in the flow of sediments downriver (Dobyns 1978, 1981). The effects that such sediments had on the biota of the lower Rio Colorado delta are unknown.

Vegetation

Up to the early 20th century, the area had a vegetation pattern clearly associated with the river. Plant communities in this area were probably similar to those currently found immediately north of the U.S. -Mexico border (Ohmart *et al.* 1988; see Nelson 1921 and Sykes 1937b for photographs). Cottonwoods (*Populus fremontii*) and willows (*Salix gooddingii*) along the banks, with shrub seepwillow (*Baccharis salicifolia*) and coyote willow (*Salix exigua*) as understory plants. Cattail (*Typha* spp.), bulrush (*Scirpus* spp.) and reed (*Phragmites australis*) formed emergent communities. Honey mesquite (*Prosopis glandulosa*) occured at a slightly higher level ("second bottom" *sensu* Ohmart *et al.* 1988), while screwbean mesquite (*Prosopis velutina*) was found along the drier banks. Arroweed (*Tessaria sericea*), salt bush (*Atriple polycarpa, A. canescens*), inkweed (*Suaeda torreyana*) and quail bush (*Atriplex lentiformis*), creosotebush (*Larrea divaricata* var. *tridentata*), ocotillo (*Fouquieria splendens*), palo verde (*Cercidium floridum*) and smoke tree (*Psorothamnus spinosus*) where found in the desert, away from the river. Additionally, both an Indian-cultivated and a wild form of the grass *Panicum sonorum* occured on the flats that were annually inundated by the river (Nabhan and de Wett 1984), and the Sonoran Desert endemic *Ammobroma sonorae* occured on sand dunes in the area. In all, the Rio Colorado delta is thought to have included 200-400 species of wetland vascular plants, most of which have disappeared (Ezcurra *et al.* 1988).

Currently, most of the massive riparian forests have disappeared, although some patches and isolated trees remain. Other plants, like cachanilla (*Pluchea sericea*) and salt bush, are widely found, even along irrigation ditches and drains. The local wild and domesticated forms of *Panicum sonorum* are ". . . for all practical purposes . . . now extinct . . ." in this area (Nabhan and de Wett 1984).

Alien plants, especially tamarisks (*Tamarix* spp.), are widespread. Tamarisks colonized the lower Colorado around 1920 from the Gila River, where they had been introduced (Ohmart *et al.* 1988). These trees cause several problems. Due to their high evapotranspiration rate they can dry out smaller water bodies, affecting fish such as the endangered pupfish (*Cyprinidon* spp.). Also, due to its aggressiveness, they outcompete cottonwoods and willows, reducing the value of the habitat for several animals, including the endangered Yuma Clapper Rail (*Rallus longirostris yumanensis*; Dudley and Collins 1995), and beavers (Mellink and Luevano 1998).

Fresh water invertebrates

Very little is known about aquatic invertebrates either before the large-scale management of the river or after it. Grinnell (1914) reported that there were no aquatic molluscs in the Lower Colorado. This seems an underestimate as, although in large erosive fluvial systems there are few bentic and sessile invertebrates, some groups are well represented, especially in areas with little water flow (Ohmart *et al.* 1988). Murphy (1917) found exoskeletons of *Planorbis tumens,* a fresh water mollusc, and *Certhidea sacrata,* a brackish water species, in the dry bed of Laguna Salada. Suggestions for other species likely to occur or to have occurred in the area can be obtained from stocks in adjacent United States (Minckley, and Marsh and Minckley, in Ohmart *et al.* 1988).

On the other hand, at least four introduced aquatic invertebrates occur in the area: Asiatic clam (*Corbicula fluminea*), paper floater mussel (*Anodonta imbecillus*), crayfish (*Procambarus,* probably *P. clarki*), and freshwater shrimp (*Palaemonetes paludosus*). The asiatic clam was introduced into the region probably in the 1950s (Bequaert and Miller 1973; Dundee and Dundee 1958; Ingram 1959; Ingram *et al.* 1964). This species is a good disperser (Ingram *et al.* 1964) and currently is very common in the area (Fox 1970; Guardado-Puentes 1975; Mellink and Luevano unpublished data). In addition to troubling irrigation systems (Ohmart *et al.* 1988), this species can negatively impact native benthic invertebrates (Dudley and Collins 1995). In southern California and Arizona, however, it is an important prey of exotic fishes (Minckley 1982) and in the Mexican portion of the delta, it appears to be an important food for racoons (*Procyon lotor,* Mellink and Luevano unpublished data).

The paper floater mussel is an alien that has been reported from the U.S. portion of the Rio Colorado. We collected shells of this species in the Mexican portion of the delta (Identifyied by Jerry Landye). A similar species, the California floater (*A. californiana*), is severely endangered in the area, very likely due to the extirpation of one of the local endemic fish species, that was obligate host for its swimming stage (Bequaert and Miller 1973).

Crayfish were introduced in the lower Colorado in the 1930s (Dill 1944) and have dispersed widely through the area since then, being abundant in the Cienega de Santa Clara (Mellink and Luevano unpublished data). Crayfish are omnivores that reduce aquatic plants and algae, invertebrates, frogs, and even some fish, and in some places have eliminated most aquatic invertebrates (Dudley and Collins 1995; Hobbs *et al.* 1989). Dudley and Collins (1995) considered it as one of the invasive species posing high environmental risks on the U.S. side of the lower Colorado. However, crayfish have been found to be an important food item for large, alien, carnivorous fish species and for the soft-shelled turtle (*Apalone spinifera*), garter snakes (*Thamnophis marcianus*), Yuma Clapper Rail, and some mid-sized mammals in the U.S. portion of the area (Minckley 1982; Ohmart 1988).

Freshwater shrimps are common in the lower Colorado, both in the U.S. (Minckley 1982) and, in Mexico, at least in the Cienega de Santa Clara (Abarca *et al.* 1993). Its actual or potential effects on the system are unknown, but some exotic fish and, to a lesser degree, American Coot (*Fulica americana*) feed on them (Eley and Harris 1976; Minckley 1982).

Fresh water fish

Thirty-seven species of fish have been reported from the U.S. side of the delta, of which only 11 are native. Ten of the native species have been extirpated or are extremely localized. Sixteen additional alien species have been introduced, but their introductions have failed (Ohmart *et al.* 1988). The first known alien in the lower Colorado was the carp (*Cyprinus carpio*), which was introduced before the turn of the century. By 1942 there were already 11 introduced fish in this area (Dill 1944; Gilbert and Scofield 1898).

The fish assemblages in the mexican portion of the delta before the construction of dams are not known, but it is clear that most native species are not faring well. A recent collection from the confluence of the Rio Colorado and the Rio Hardy produced 13 species of fish, 11 of them alien. The two native fish were the striped mullet (*Mugil cephalus*), and the machete (*Elops affinis*), both typical of brackish waters (Valle-Rios 1997).

The modification of aquatic habitat, especially through damming, and the predation by alien fish on larvae are thought to be the principal causes of the demise of the native species of fish (Ohmart *et al.* 1988). Alien fish can also predate on very localized spring snails (Hydrobiidae), amphibians, and the endangered pupfish (Dudley and Collins 1995). However, alien fish are not the only ones that feed on native pupfish, as the native machete also does so (Dill 1944).

Icthyological research in the area has focused on the local pupfish (*C. macularius*), mostly in the Cienega de Santa Clara and in the artesian wells along the Cerro Prieto fault (Abarca *et al.* 1993; Hendrickson and Varela-Romero 1989). This species is adapted to variable environments and is a good colonizer of new habitats, and the delta populations are reasonably healthy (Hendrickson and Varela-Romero 1989). However, changes in the quality of the water reaching the Cienega and the abundance of alien fishes are imminent threats to their survival (Abarca *et al.* 1993; Glenn *et al.* 1992; Hendrickson and Varela-Romero 1989; Ohmart *et al.* 1988; Rinne and Guenther 1980). The following alien fish species have been found in the Cienega de Santa Clara (Abarca *et al.* 1993): *Notropis lutrensis, Poecilia latipinna, Gambusia affinis, Tilapia* sp. In addition to some of those species, the artesian wells have also *Oreochromis* spp., *Cyprinus carpio,* and *Ictalurus punctatus.* Striped mullets and other estuarine fishes are found in the main body of the Cienega as well as in channels that have some influx of seawater.

Amphibians

Limited collecting effort has been made to document the amphibians on the Mexican side of the delta, and the list of potential species must be extrapolated from nearby Arizona and California (Bury and Luckenbach 1976; Grismer 1994; Ohmart *et al.* 1988; Vitt and Ohmart 1978; Zeiner *et al.* 1988). There is even less information on the status of the different species in the area.

Six native species of amphibians could have occurred in the area (Mayhew 1962; Ohmart *et al.* 1988; Van Denburg and Slevin 1913; Vitt and Ohmart 1978): Couch's spadefoot (*Scaphiopus couchi*; of which no specimens exist from the Mexican side of the Rio Colorado), Great Plains toad (*Bufo cognatus*), red-spotted toad (*B. punctatus*), Woodhouse toad (*B. woodhousii*), Sonoran Desert toad (*B. alvarius*; of which only one specimen has ever been collected - Brattstrom 1951) and lowland leopard frog (*Rana yavapaiensis,* of the *R. pipiens* complex). None of them requires running water, although two prefer it, but they all require stagnant water during the breeding season. The species that depend less on water are Couch's spadefoot, Great Plains toad, red-spotted toad, and Woodhouse toad. Except for the red-spotted toad, agriculture could have benefited these species, at least at some time (Ohmart *et al.* 1988). In fact, the Great Plains toad commonly occurs in irrigation channels (Vitt and Ohmart 1978).

The two other species, Sonoran Desert toad and lowland leopard frog, prefer permanent or semipermanent water, although they are found in a variety of habitats and can use ephemeral reservoirs (Zeiner *et al.* 1988). It is possible that the reduction in flow in the Rio Colorado has impacted negatively these two species.

The lowland leopard frog has not been recorded recently in the U.S.-Lower Rio Colorado but its rarity or, perhaps, extirpation from southern California has been linked to the introduction of bullfrogs (*Rana catesbeiana*) to the area, rather than to river modification (Vitt and Ohmart 1978). The Rio Grande leopard frog (*R. berlandieri*) could also be responsible for the status of the lowland leopard frog (see Platz *et al.* 1990).

The bullfrog has been introduced to many areas for its commercial production. In California, it diseminated rapidly through the whole state (Jennings 1983; Storer 1922). It was introduced to the Lower Colorado in the 1920s (Dill 1944), where it is currently abundant (Grismer 1994; Vitt and Ohmart 1978), and it is raised on a farm adjacent to the Rio Hardy. The bullfrog is the introduced amphibian with largest biological impact because of its aggressive, generalist, and predatorial behavior (Bury and Luckenbach 1976; Dudley and Collins 1995). In one case its diet included crayfish, wolf spiders (Lycosidae), insects (including a scorpion), abundant coleoptera, and also muskrats, snakes, soft-shelled turtles, and Asiatic clam (Clarkson and De Vos 1986). The introduction of bullfrogs has caused the disappearance of native amphibians (Clarkson and De Vos 1986; Hammerson 1982; Moyle 1973).

Rio Grande leopard frog and Tiger salamander (*Ambystoma tigrinum*) have also been introduced to the area. The Rio Grande leopard frog exists in the U.S. portion of the Lower Colorado (Ohmart et al. 1988, Platz *et al.* 1990), and very likely also in adjacent Mexico. Its effects have not been studied, but it could affect native amphibians (Platz *et al.* 1990). The tiger salamander is commonly used as fishing bait, and it is often released in fishing areas. So far two specimens from near Yuma are known (Vitt and Ohmart 1978). Their larvae compete with those of native amphibians (Zeiner *et al.* 1988).

Reptiles

Only two native species of aquatic reptiles occurred in the Lower Colorado: the Sonoran mud turtle (*Kinosternon sonoriensis*), which has never been collected on the Mexican side of the border, and the checkered garter snake (*Thamnophis marcianus*). Records of yellow mud turtle (*K. flavescens*) have been dismissed as invalid (Funck 1974; Jennings 1983; Van Denburg and Slevin 1913; Vitt and Ohmart 1978). Ohmart *et al.* (1988) also include Mexican garter snake (*T. eques*) as present in the area, but we have not been able to find any suportive records, and likely this was based on a misidentification. The Sonoran mud turtle could have been extirpated from the area, and the checkered gartner snake diminished in its numbers, due to the reduction of riparian habitat (Jennings 1983; Ohmart *et al.* 1988). Garter snakes occur in some irrigation ditches, but there they are killed by locals, children and pets.

At least three species of alien reptiles have been introduced into the Lower Colorado: the soft-shelled turtle (*Apalone spinifera*), the painted turtle (*Crysemys picta*) and the American alligator (*Alligator mississipiensis*). Soft-shelled turtles were introduced into the Lower Colorado probably at the turn of the century (Bury and Luckenbach 1976; Dill 1944; Miller 1946; Webb 1962). This species was abundant throughout Valle the Mexicali, but, according to local inhabitants, hunting for human consumption has reduced its populations.

Painted turtles were not reported for California by Bury and Luckenbach

(1976), but recently they have been found in the Mexican portion of the Colorado River (L. Grismer, pers. com.), as well as in southwestern California (Dudley and Collins 1995). Free-living painted turtles surely derive from released pets. The potential threats of this species are undocumented, although it may have threatened native frogs and the southwestern pond turtle (*Clemmys marmorata pallida*) in southwestern California (Dudley and Collins 1995).

American alligators were released during the late 1930s and early 1940s in at least two occasions in the U.S. portion of the Lower Colorado, by a traveling circus, and at the railroad station at Needles where they had been kept as pets (Hock 1954). The name "El Caiman" (the Alligator) for a ranch along the Rio Pescaderos, in Baja California, suggests that at least one of them traveled south through the riverine system.

Birds

Ohmart *et al.* (1988) considered both fish and birds as the animals most impacted by the transformation of the lower Rio Colorado Valley, in the U.S.A. For the Mexican side of the area little is known about the birds. Even Nelson's (1921) description of the peninsula largely overlooks the aquatic birds of this area. The early century synthesis by Grinnell (1928) is the most comprehensive review. A later synthesis (Wilbur 1987) has been criticized (Everett 1988), and recently only a few, localized observations have been published (v.gr. Mellink *et al.* 1996, 1997; Palacios and Mellink 1992, 1993; Patten *et al.* 1993; Peresbarbosa and Mellink 1994; Price 1899; Ruiz-Campos and Rodriguez-Meraz 1997). As an alternative, the information from the U.S. side of the delta is a useful complement in many cases.

One of the birds that has conservation problems is the Large-billed Savannah Sparrow (*Ammodramus sandwichensis rostratus*). This subspecies breeds solely in marshes of the delta of the Rio Colorado and, perhaps, in some marshy areas of northwestern Sonora (Van Rossem 1947). During the non-breeding season it used to disperse widely, becoming very abundant even in San Diego, California. Currently, it is almost absent from that city, a fact that has been linked to the modifications of the delta (Unitt 1984). The species still nests on Isla Montague, at the mouth of the river (Peresbarbosa and Mellink 1994), but its nesting habitat elsewhere appears very reduced.

Formerly, the delta supported important colonies of nesting waders, especially of Snowy Egrets (*Egretta thula*) and Great Egrets (*Ardea alba*). There was a strong reduction of these colonies early in the century due to their hunting, although recently some new colonies have formed (Kathy Molina, pers. com.; Mora 1989, 1997), and others are found on Isla Montague (Palacios and Mellink 1992, 1993; Peresbarbosa and Mellink 1994). The most common waders in the area currently are Black-crowned Night-heron (*Nycticocorax nycticorax*), Green Heron (*Butorides striatus*), Snowy Egret, Great Egret, and Great Blue Heron (*A. herodias*). Only one alien species of waterbird has colonized the area: the Cattle Egret (*Bubulcus ibis*), which breeds in Valle de Mexicali since the early 1970s (Mora 1997), and which is increasing in numbers in the region (Garrett and Dunn 1981; Rosenberg *et al.* 1991).

Nothing is known about the current occurrence of more sporadic species like the Roseate Spoonbill (*Ajaia ajaja*) documented and collected early in the century at Laguna Salada (Grinnell 1926; letters of E.W. Funcke to J. Grinnell, of 17 December 1925, 31 December 1925, and 5 January 1926 at the Museum of Vertebrate Zoology, University of California, Berkeley). Similarly, there are no recent records of Wood Storks (*Mycteria americana*), but they have likely been overlooked in the area (Wilbur 1987).

Waterfowl intensively use Valle de Mexicali and some species could have increased populations as a result of agriculture (Anderson and Ohmart 1982; Mellink *et al.* 1997; Ohmart *et al.* 1985). The waterfowl have been described by several authors (A. Leopold 1949, 1953; A.S. Leopold 1959; Kramer and Migoya 1989; Payne *et al.* 1991; Saunders and Saunders 1981), and their discussion is beyond the scope of this article. We will comment only on the Fulvous Whistling-duck (*Dendrocygna bicolor*). This species was recorded from the area in 1922 (Bancroft 1922). It is currently a fairly common but declining, summer resident with some winter records at some locations on the U.S. side of the lower delta (Garrett and Dunn 1981; Rosenberg *et al.* 1991), but there are no modern records of it in the Valle de Mexicali.

Shorebirds are an important part of the fauna of the delta, especially on the extensive intertidal mudflats south of Isla Montague (Mellink *et al.* 1997). Within the delta there are some large mudflats to the south of the Cienega de Santa Clara which also support large amounts of shorebirds (Abarca 1993; Mellink *et al.* 1997; Morrison *et al.* 1992). The abundance of shorebirds in the entire delta has promoted recognition of the area by the Western Hemisphere Shorebird Reserve Network. It is unknown whether original conditions of the area supported more or less shorebirds than today, and of which species.

One of the most sensitive birds of the delta is the Yuma clapper rail (*Rallus longirostris yumanensis*), whose population in Cienega de Santa Clara is almost 50% of the known population of the subspecies (Abarca *et al.* 1993; Eddleman 1989). Some minor populations of this rail may occur in some vegetated agricultural drains throughout the valley (Robert Henry, pers. comm.).

Mammals

The three aquatic mammals of the lower delta, river otter (*Lutra canadensis*), beaver (*Castor canadensis*), and muskrat (*Ondatra zibethica*), have been considered at risk due to the modification of the water streams (Ceballos and Navarro 1991). Huey (1964) did not report river otters in Baja California, and Ohmart *et al.* (1988) considered that they had never been abundant in the Lower Colorado (U.S. portion). However, Sandez (in Herrera-Carrillo 1932) indicated that they were abundant in Valle de Mexicali sometime during the 19th century, a statement that Mellink (1995) found difficult to qualify. Later, Onesimo Gonzalez (Campo Flores, Rio Hardy) described and positively identified river otters in a field guide, and indicated that they had been abundant in the Hardy river until about 1955, when they disappeared (Mellink and Luevano unpublished data). There are no river otters currently in the area, and the habitat seems not suitable to them.

One of the most typical and abundant species of the Lower Colorado was the beaver (Huey 1964; MacDougal 1906; Pattie 1931; Stone and Rhoads 1905). Currently its populations on the Mexican side of the delta are largely reduced, and highly variable. They expand and contract with the amount of free water in the area, and some years the species probably disappears altogether, or almost so.

When the system receives water (i.e. when large amounts of water are released from U.S. dams), large colonies can again establish, either from animals that have survived in localized water pockets or from animals carried from the U.S. by the sudden river current (Mellink and Luevano 1998).

Muskrats seem to have been rather uncommon in the Lower Colorado early in the century (Mellink 1995). Muskrats require still waters and were favored by the establishment of agriculture in the area (Dixon 1922; Grinnell 1914; Mellink 1995). Their maximum populations in the area occurred probably during the 1960s, when cultivated land was at its largest, and the water conduction system was inefficient with many seeps. Although the lining of channels with concrete surely reduced the populations of this species, the species does not seem to face any conservation problem (Mellink 1995), despite its listing by Mexico as a species at risk.

Concluding remarks

The basic premise for protecting the area was its alleged "pristinity". However, it is clear that the area is far from biologically intact. Even the Cienega de Santa Clara, touted as one of the last remnants of Rio Colorado Delta wetlands, owes its condition to the recent discharge of brine water from the Wellton Mohawk Irrigation District, in Arizona, through the Wellton Mohawk Main Outlet. The biological composition of the area's wetlands includes several alien species and is quite different from that of turn-of-the-century. Clearly, the conditions that make an area legally suitable for being a Biosphere Reserve, under the Mexican Environmental Law, do not exist in the Rio Colorado Delta.

On the other hand, several species of animals from the area are considered as rare, threatened, or endangered in a Baja California state government brochure, a poster from the local university, the official list of species at risk, and a list in a recent hunting calendar. Some species in the area undoubtedly face conservation problems, like the pupfish. However, the listing of several other species seems to be based either on wrong perceptions of their local conditions or based on their status elsewhere. For example, the soft-shelled turtle, although it could have a problem in northeastern Mexico, is alien to the delta and should not be listed for it. Also, the listing of muskrats for this area is not consistent with its present status.

Legal protection actions have been focused on the two marine species, totoaba and vaquita, which are perceived as at greater risk. They have been protected by multiple measures, including restrictions in the type of fishing gear and its use in the delta area. The decree of a large area as a Biosphere Reserve has meant stricter enforcement of such existing fishing restrictions. This stricter enforcement and the establishment of a small research station, have been the only actions toward biological conservation in the area. No management measures have been taken for any other species at risk, including such flag-species as the pupfish and Yuma Clapper Rail, except for listing them and prohibiting their hunt. Indeed, there hasn't even been a serious effort to evaluate the current status of the regional species and subspecies presumably at risk.

Although the area is biologically very modified, it can provide important opportunities for the conservation of wetland taxa. The first step should be a thorough evaluation of the status of the species or subspecies presumed to be at risk, and the determination of the factors that affect them. Only then can adequate management actions be taken.

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Benthic Communities and the Invasion of an Exotic Mussel in Mission Bay, San Diego: A Long-Term History

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Abstract.—A twenty-year dataset on the subtidal benthic macrofauna within Mission Bay, San Diego, reveals distinct differences in community structure along a back-bay/front-bay gradient. Assemblages in the extreme back bay are characterized by low diversities and abundances, and are dominated by an exotic mussel, *Musculista senhousia.* Species richness increases toward the mouth, and because of the very high densities of *M. senhousia* at a station intermediate in the spatial gradient, total abundance and biomass show sharp peaks in this region. Despite the dramatically increased dominance *M. senhousia* has achieved in the bay, few negative effects of this invasion on subtidal macrofauna are evident.

Coastal bays, estuaries, and lagoons located within cities are subject to a wide variety of anthropogenic influences, including habitat loss or alteration, pollution, and the invasion of exotic species (e.g. Conomos 1979; Essink and Beukema 1986; Cohen and Carlton 1998). Many coastal embayments within southern California have been particularly affected by urbanization (Marcus 1989; Schoenherr 1992; Anderson et al. 1993). Yet, these systems are vital as their remnant natural habitats support several endangered species and are the sites of active restoration and conservation efforts (Zedler 1996).

One of the most highly modified systems in southern California is the 1862-ha coastal lagoon, Mission Bay, in San Diego (Fig. 1). Over the last 150 years, the bay has been extensively altered by river diversion, dredging, and filling, and it now is the largest aquatic park on the west coast of the United States (Chapman 1963; California Coastal Commission 1987; Crooks 1998a). The physical and hydrographic characteristics of the bay produce a flushing gradient, with relatively high water exchange near the mouth (San Diego City Planning Department 1957; Taylor 1982; Marcus 1989; Largier et al. 1997). In the back bay, flushing is more sluggish due to the increased distance from the ocean and the presence of a large, artificial island (Fiesta Island) which creates two narrow, dead-end channels (San Diego Water Utilities Department 1978). Drift tube and fluorescene dye studies also suggest higher retention times for this region (Levin 1983). Compounding circulation problems in the back bay is the input of organic-rich urban runoff from two creeks in this area (San Diego Water Utilities Department 1978; Marcus 1989). Mission Bay is seasonally hypersaline, with warmer waters and slightly

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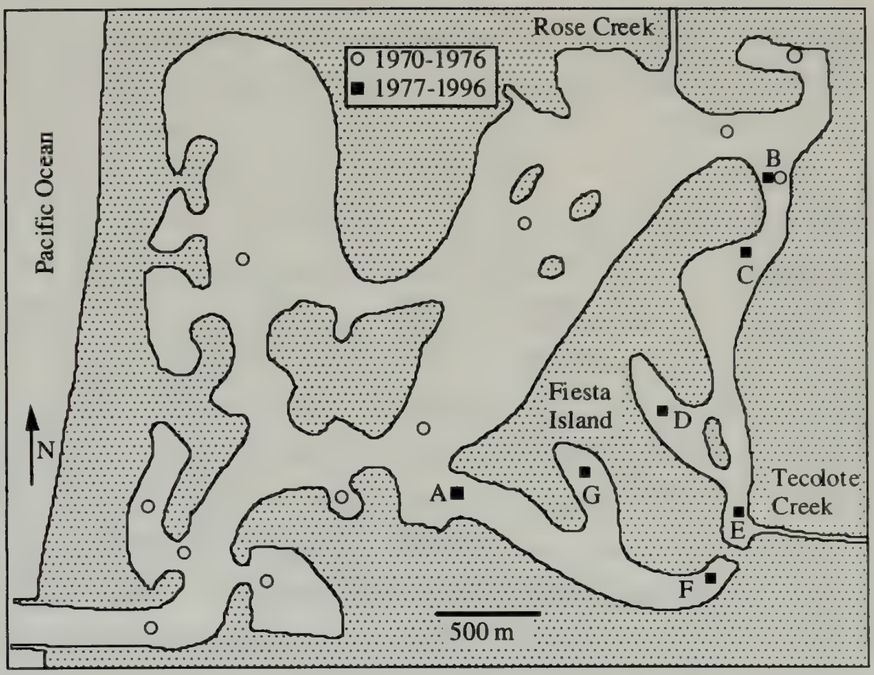

Fig. 1. Mission Bay, San Diego, California (32°47′N, 117°14′W), showing sample sites in this and a previous study (Dexter 1983).

higher salinities in the back bay during the summer months (Levin 1983). Such conditions, which are typical of systems in regions with Mediterranean climates, may further serve to reduce bay-ocean mixing (Largier et al. 1997). During winter months, salinities in the back bay can be periodically decreased after heavy rains, but the salinity of the entire bay often is near full seawater (Levin 1982).

One of the most dramatic changes in the biotic nature of coastal systems within California has been the invasion of exotic species (Carlton 1979; Cohen and Carlton 1998; Crooks 1998a). Although marine systems in San Diego appear less heavily invaded than in San Francisco Bay, there are approximately 60 non-native marine species recognized from the region (Crooks 1998a). One of the most conspicuous of these invaders is a mat-forming mytilid, *Musculista senhousia* (Benson in Cantor) (Crooks 1992, 1996). Within Mission Bay, the presence of this accidentally-introduced mussel was first noted in a salt marsh creek in the mid-1960's (MacDonald 1969). Since then, the short-lived, fast-growing mussel has become abundant in both intertidal and subtidal soft sediments (Dexter 1983; Crooks 1996, 1998b), and has been reported to have both positive and negative effects on macrofauna and eelgrass (Crooks 1998a; Reusch and Williams 1998).

The goal of this paper is to describe long-term spatial and temporal trends in the subtidal benthic communities of Mission Bay. Within the bay, regular sampling of the subtidal, soft-bottom benthos, conducted in conjunction with a course in Biological Oceanography at San Diego State University, began in 1970. During the first 8 years, sampling was carried out close to the entrance of Mission Bay (Dexter 1983). Beginning in 1977, sampling began around Fiesta Island at sites situated increasing distances from the mouth and ending at the dead-ends of the two passages (Fig. 1). We will use these data to 1) identify dominant species in the bay and assess spatial and temporal trends in these taxa, 2) characterize differences in community structure (including species richness, total biomass, total abundances, and representation of suspension and deposit feeders) along the back-bay/front-bay gradient, 3) describe the population dynamics of *Musculista sen-*

housia in the subtidal of the bay by examination of size-frequency data, and 4) identify changes in biotic communities potentially attributable to this invader.

Methods

Field and Laboratory Procedures

In 1977, seven stations were established at locations around Fiesta Island (Fig. 1). One of these, Station B, was an original station (Dexter 1983). Stations were located at least 500 m apart and were identified with reference to shoreline positions, and all samples were taken within a ca. 15-m radius at each station. Sampling was conducted on 16 dates from 1977 to 1996, occurring primarily in the late summer or winter. Stations A,B,C, and F were sampled on every date (16 times), Station E was sampled on 14 dates, and Stations D and G were sampled 11 times each. On each sampling date, four to seven replicate grab samples of approximately 0.1 m^2 surface area were taken at the stations. Although the number of replicate sub-samples (i.e. grabs) varied between years, the same number of replicates were taken at all stations sampled on a given date. The Hayward orange-peel grab used for sampling penetrated approximately 15 cm into the substrate. A total of 463 grabs were collected, and the mean sample volume was 4.501.

Collected sediment was wet sieved through 750-μm mesh, and material retained on the sieve was stained with rose bengal and preserved in 5% buffered formalin. Samples were sorted under a dissecting microscope, and all macrofauna were transferred to alcohol, counted, and identified to the lowest taxonomic level possible. All collected specimens from each core were wet-weighed together to provide a total biomass of the sample. This information was used to characterize macrofaunal communities in terms of species richness, total density of individuals, densities of major macrofaunal taxa, and total biomass. In addition, feeding modes of species were determined from the literature (Fauchald and Jumars 1979; Morris et al. 1980). As the mesh size used in this study (750 μm) was larger than that often used for collecting macrofauna (300–500 μm), the values in this study represent underestimates of macrofaunal densities and species richnesses. However, consistent spatial and temporal comparisons of sampled communities are possible as the same mesh size was used throughout the study.

Certain species were identified as community dominants, and their distribution and abundances were selected for further analysis. The following criteria were applied to determine community dominants. The species 1) was present at one or more stations on at least 90% of the sample dates between 1977 and 1996, 2) comprised at least 5% of the individuals, and 3) was present on at least 40% of the sample dates at any single station.

In order to investigate the population dynamics of *M. senhousia,* lengths of the mussel were measured to the nearest 1 mm using vernier calipers on all intact specimens, unless very large numbers were collected. In these cases, a plankton splitter was used to subdivide large samples to obtain an unbiased representative subsample of 100–200 individuals.

Data Analyses

In this study the sampling unit was a station, and station means were used for spatial and temporal comparisons. For calculations of means and standard errors, data were log (x+1) transformed and subsequently back-transformed for graphical presentations. Spearman rank correlations were performed to examine relationships among the dominant species, and were calculated using means from each station on each sampling date ($n = 100$ for each correlation). To detect only highly significant relationships and to take into account the number of comparisons made (twenty-eight), only correlations with a $P < 0.001$ are reported. Similarities of communities were calculated using Bray-Curtis coefficients of community similarity (Krebs 1989). Both the spatial variation among replicates within a station at any one time (i.e. within-sampling unit variability) and temporal variation at a station over time (i.e. comparisons of communities at a station among years) were examined. Also, paired t-tests were used to compare coefficients of variation of densities of suspension and deposit feeders.

In order to investigate general relationships between the communities at the sites, an ordination technique, non-metric multi-dimensional scaling (MDS), was used (Clarke and Warwick 1994; ter Braak 1995). In this technique, Bray-Curtis similarities were calculated comparing the community at each site to that at each other site. Using this matrix of similarities, the MDS technique provided the best two-dimensional configuration for each station relative to all other stations. This technique also yielded a stress value to indicate the level of fit of this two-dimensional representation (values less than 0.1 typically are considered good). The first MDS plot compared all stations, with data averaged across all years (using only dates in which all stations were sampled). The second compared the five most frequently sampled stations, using the averages of samples from summer months and the averages of samples from winter months. Data for MDS analyses were non-transformed and non-standardized. SIMPER (similarity percentage) analyses (Clarke and Warwick 1994), a resampling technique, also were performed to determine the contribution of individual species to community dissimilarities.

Results

Dominant Species

The macrofauna (<750 μm) of Mission Bay were dominated primarily by molluscs and polychaetes; the two groups combined accounting for 75 to 91% of all fauna at the stations. Station A, closest to the mouth, had the most distinctive representation of these taxa, with 84% polychaetes and 4% molluscs. All other stations had between 32–45% molluscs and 30–55% polychaetes.

Eight species (or species complexes) were identified as community dominants (Fig.'s 2 and 3). These included three suspension feeders, one carnivorous polychaete, and four polychaete deposit feeders. Averaged over all sampling dates, the eight dominants together accounted for 92% of all individuals at Station B, 82% at Station C, and 65–70% at the other stations. The deposit-feeding polychaete *Lumbrineris* sp., which was identified as the community dominant in the earlier studies of Mission Bay (= *L. minima* in Dexter (1983)), was still widely distributed throughout the bay, with consistently high population densities at Station A (Fig. 2). Another deposit-feeder, the maldanid *Praxillella pacifica* Berkeley, a large, head-down conveyor belt feeder, was rare at most stations but attained high densities at Station A. *Tharyx* sp. was present at low densities at most sta-

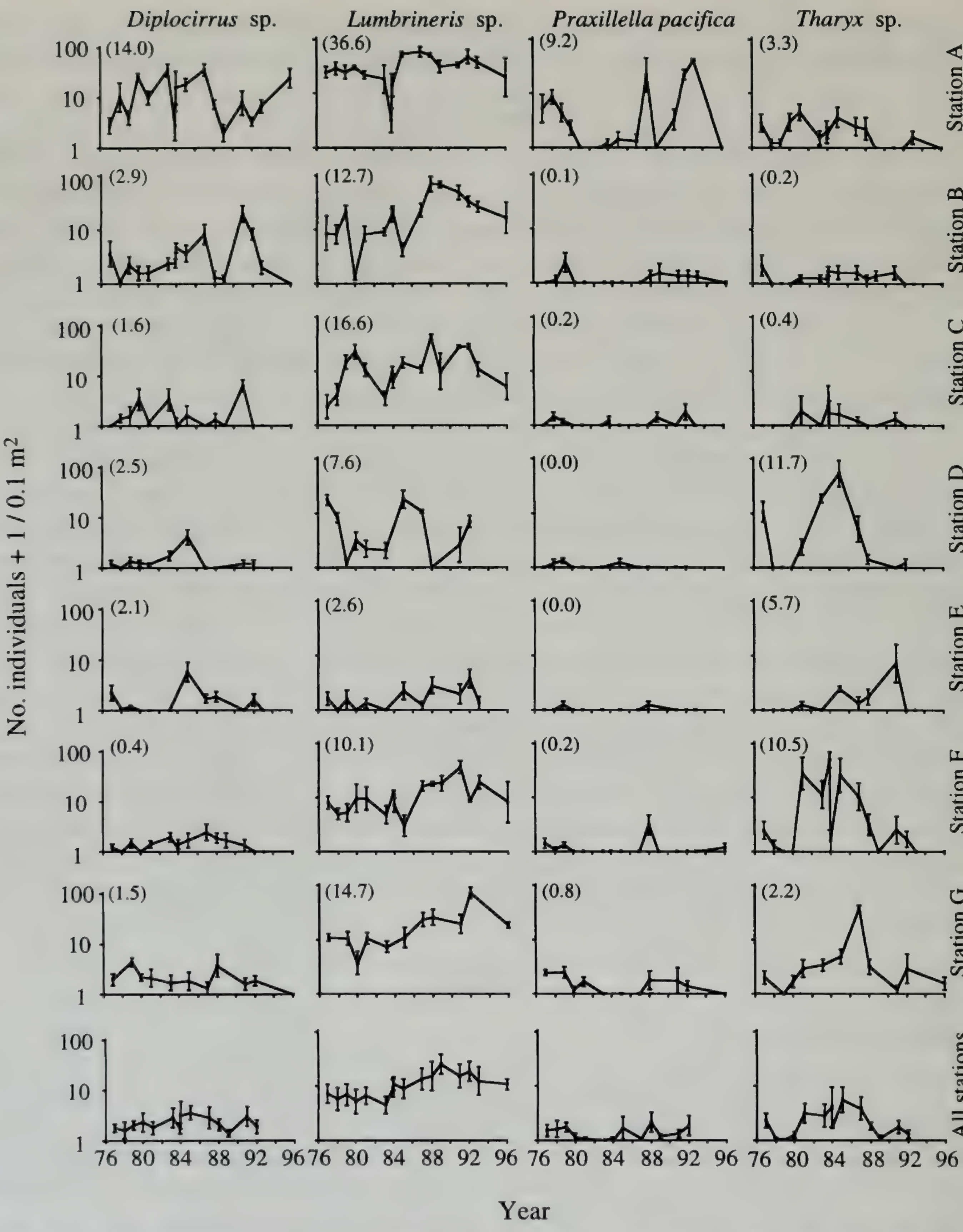

Fig. 2. Mean abundances (± 1 s.e.) of the dominant deposit-feeding species. Numbers in parentheses represent contribution of the species to total number of individuals at the station, averaged across all sampling dates.

tions, and reached highest densities at Stations D and F. The flabelligerid *Diplocirrus* sp. (=*Pherusa neopapillata* in Dexter (1983)) occured at low densities at all stations except Station A. The suspension-feeding sabellid *Euchone limnicola* Reish was present at all stations, although it occured infrequently and at low densities at Stations D and E (Fig. 3). The populations of the phoronid *Phoronis* sp. fluctuated widely; highest densities occured at Station B and lowest densities at Station A. The invasive mussel, *Musculista senhousia,* showed a general pattern

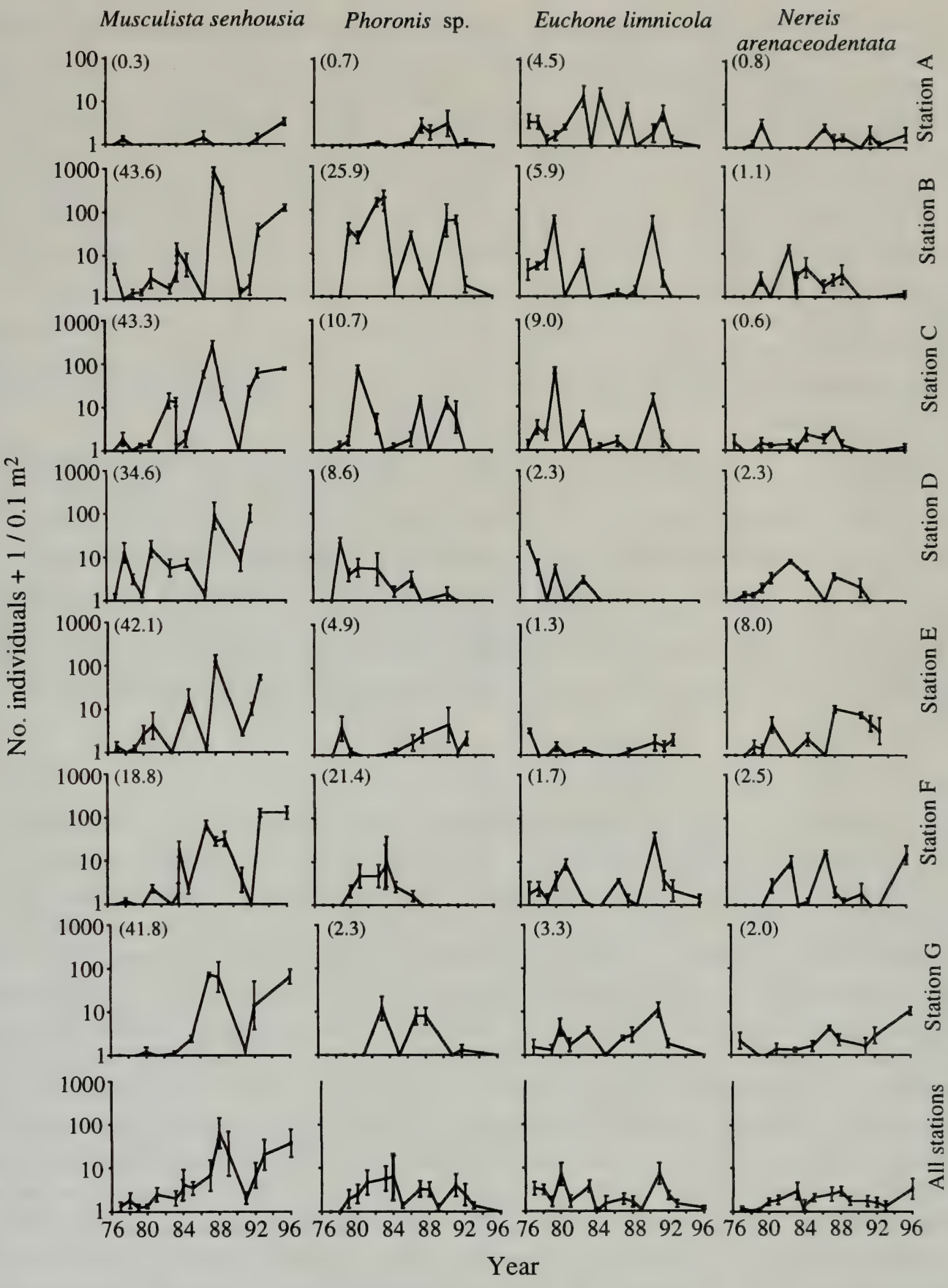

Fig. 3. Mean abundances (± 1 s.e.) of the dominant suspension-feeding and carnivorous (*Nereis arenaceodentata*) species. Numbers in parentheses represent contribution of the species to total number of individuals at the station, averaged across all sampling dates.

of increased abundance over time at all Stations except A, where it was rare. Densities of the predatory polychaete *Nereis arenaceodentata* Moore were generally the lowest of all the dominant species, but it was persistent throughout most stations with less frequent occurence at Station A.

There were significant Spearman rank correlations ($P<0.001$) among the distribution of some of the community dominants. *Musculista senhousia* correlated negatively with the suspension-feeding polychaete *E. limnicola* (r = −0.36) and the deposit-feeding polychaete *Diplocirrus* sp. (r = −0.29), and positively with the predatory polychaete *N. arenaceodentata*(r = 0.42). The deposit-feeding maldanid *Praxillella pacifica* correlated negatively with *Phoronis* sp. (r = −0.36) and positively with *Lumbrineris* spp. (r = 0.44). These relationships may represent possible interspecific interactions as well as differences in habitat utilization. For example, the negative correlation between *Phoronis* sp. and *Praxillella pacifica* may represent different habitat preferences as the former was rare at Station A whereas the latter was most abundant there (Fig.'s 2 and 3). These correlations also reflect temporally disjunct species occurences at the same station, such as is evident between *M. senhousia* and the polychaetes *E. limnicola* and *Diplocirrus* sp. (Fig.'s 2 and 3).

Occasionally, other species were abundant in the benthos (i.e. comprising greater than 20% of the individuals at a station). These included the gastropod *Acteocina inculta* (Gould) (Stations C and F in 1977; Station D in 1979), the polychaetes *Leitoscoloplos pugettensis* (Pettibone) (= *Haploscoloplos elongatus* in Dexter (1983); Station E in 1980), *Chaetozone corona* Berkeley and Berkeley (Stations F and G in 1980), and *Armandia brevis* (Moore) (Station E in 1991), an unidentified turbellarian flatworm (Station E in 1981), the amphipod *Aoroides columbiae* Walker (Station E in 1981), and the isopod *Paracerceis gilliana* (Richardson) (Station D in 1985).

Back Bay—Front Bay Gradient

Examination of dominant species and community characteristics reveal differences in the stations (Table 1; Fig.'s 2 and 3). From this information, Stations A, B, and E can be identified as being relatively distinct. Station E, the poorly-flushed site at the mouth of Tecolote Creek, had the lowest species richness, biomass, and total density (Table 1). Suspension feeders (primarily *M. senhousia*) and deposit feeders were in comparable abundances at this station (Fig. 4). Replicate grabs at this station displayed low similarities, indicating high within-sampling date spatial variability (within-year similarities, Table 1). Similarly, the average similarity of communities across time also was the lowest of all stations, suggesting high temporal variability in this part of the bay (between-year similarities, Table 1). Station B, at the northern end of Fiesta Island, had the highest averages of biomass, macrofaunal density, and species richness (Table 1). Spatial variation within sampling dates was relatively low, but temporal variation at the station was larger (Table 1). Station A, closest to the entrance, had the most distinct representation of the dominant benthic macrofauna (Fig.'s 2 and 3). Species richness at the station was relatively high, biomass relatively low, and density intermediate (Table 1). Also, deposit feeders (e.g. *Diplocirrus* sp. and *Lumbrineris* spp.) consistently outnumbered suspension feeders (Fig. 4). The communities at this station displayed relatively low spatial and temporal variability, with the highest averages of within-year (along with Station B) and between-year coefficients of similarities (Table 1).

MDS of the average species compositions provides another perspective on relationships of communities at the stations, and reveals patterns in community structure which correspond to the back-bay/front-bay gradient (Fig. 5A). The two

Table 1. Benthic community characteristics and within-station similarities. Data are means ± 1 s.e.

Characteristics	Stations						
	A	B	C	D	E	F	G
A) Community Characteristics							
Density (no./m^2)	941 ± 140	2166 ±623	869 ± 230	902 ± 189	379 ± 134	847 ± 161	996 ± 320
Biomass (wet weight (g)/m^2)	23 ± 5	114 ± 32	87 ± 31	47 ± 14	13 ± 5	109 ± 47	100 ± 45
Species richness (no./m^2)	11.1 ± 1.2	11.8 ± 0.8	8.0 ± 0.9	9.1 ± 0.7	4.9 ± 1.0	7.3 ± 0.9	10.1 ± 1.7
B) Within-station Similarities							
Within-year	0.56 ± 0.02	0.56 ± 0.03	0.55 ± 0.04	0.41 ± 0.03	0.30 ± 0.06	0.44 ± 0.03	0.46 ± 0.04
Between-year	0.51 ± 0.04	0.32 ± 0.01	0.33 ± 0.05	0.24 ± 0.05	0.21 ± 0.05	0.28 ± 0.05	0.34 ± 0.05

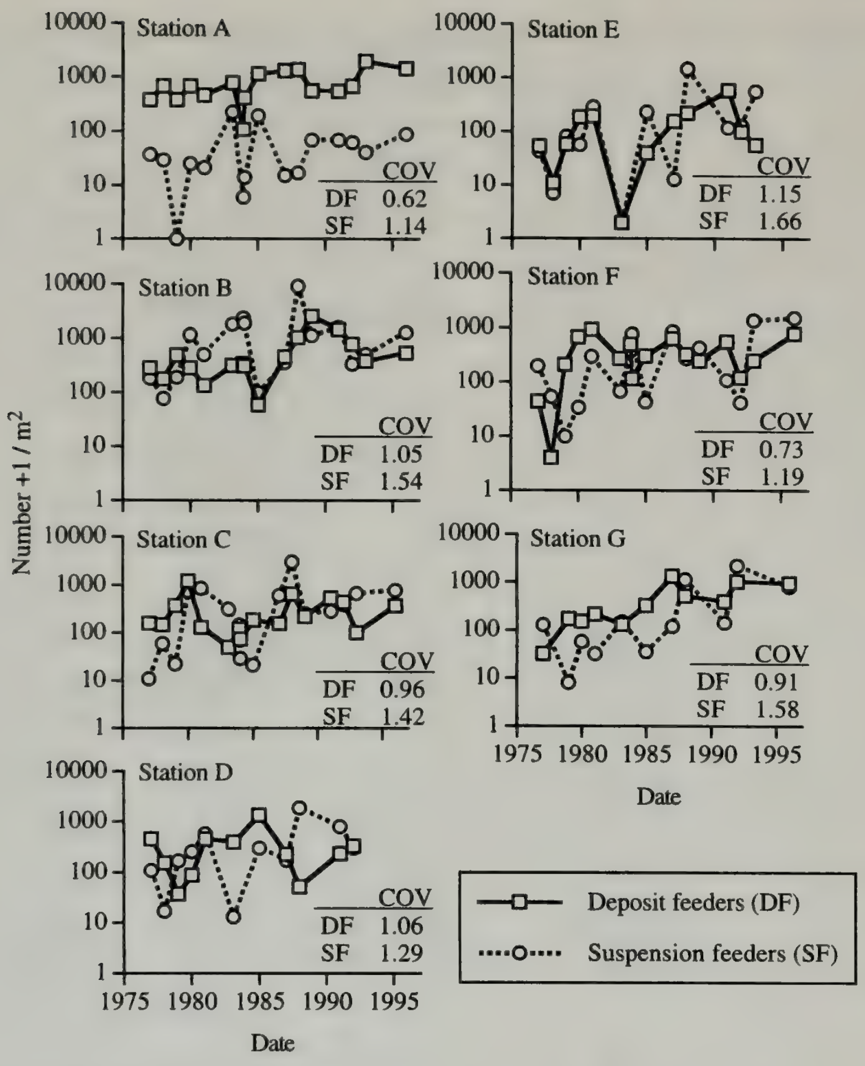

Fig. 4. Average densities of suspension feeders and deposit feeders over time. Coefficients of variation (COV) also are provided.

most distant stations, A and E, appear most distinct. The other stations cluster in the middle, with Station B most similar to Station A. Stations G and D, which both reside in small coves on different sides of Fiesta Island, also appear relatively similar to each other. The analysis of five stations in summer and winter months reveals seasonality in the faunal communities, but the back-bay/front-bay gradient observed in the overall MDS (Fig. 5B) is evident in both seasons. Station A had the highest similarity between the summer and winter months, while Station E had the lowest similarity.

SIMPER analyses between stations A, B, and E (Table 2) demonstrate how differences in abundances of dominant species (Fig.'s 2 and 3) drive seasonal community dissimilarities. In summer months, *M. senhousia* is most important in driving differences among the three stations, and *Praxillella pacifica* distinguishes Stations A from both B and E. The polychaete *Lumbrineris* sp. was responsible for differences among all stations in both summer and winter. In winter, *Diplocirrus* sp. distinguishes the front-bay from the back-bay stations, and *Phoronis* sp. distinguishes Stations B from A and E.

Examining all stations together, some general patterns emerge. The average within-year and between-year similarities (Table 1) were correlated ($R^2 = 0.68$ using exponential regression), indicating that stations that were spatially variable at any one time also were variable over time. Also, suspension feeders showed relatively large temporal variability (Fig. 4), with an average coefficient of vari-

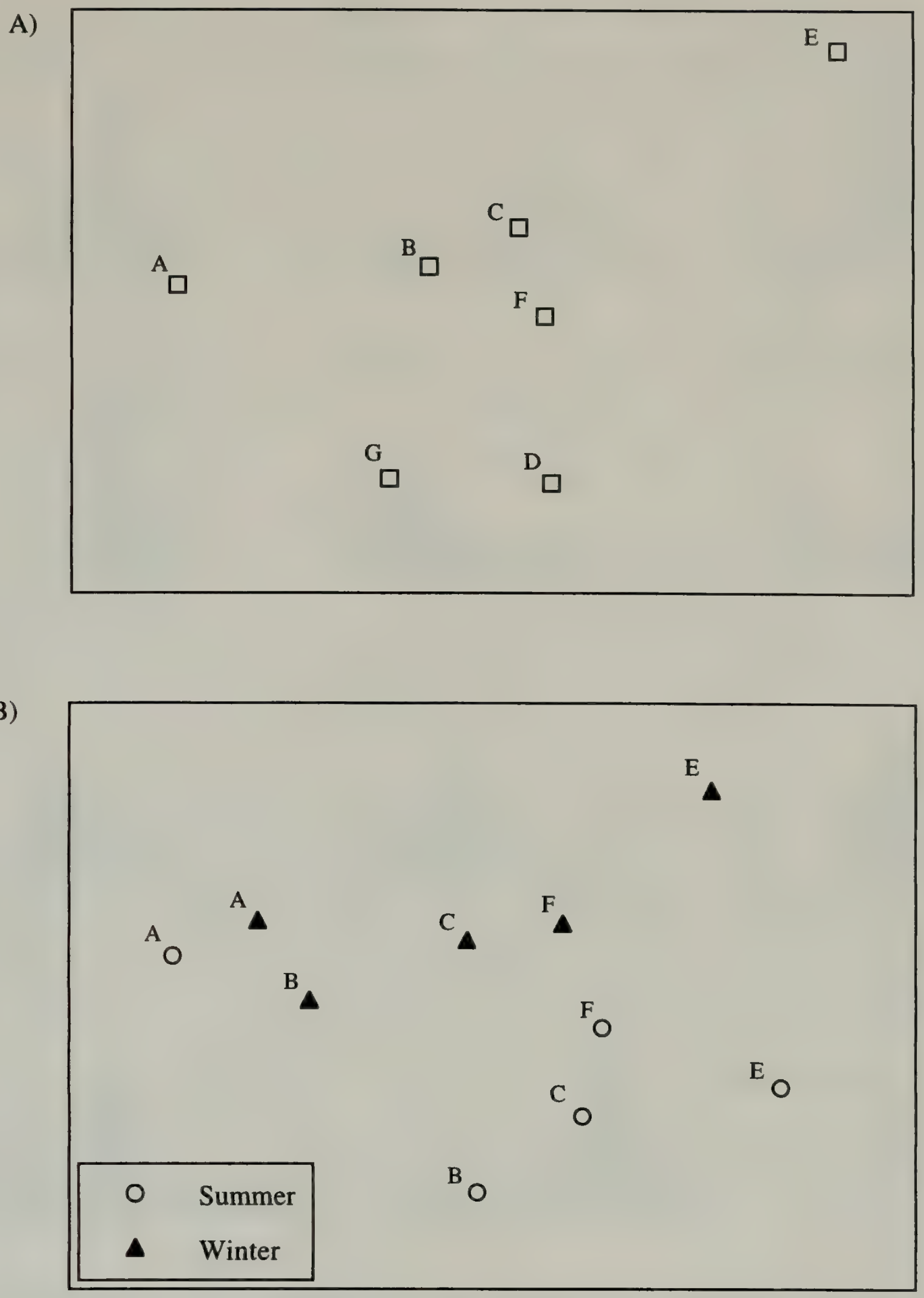

Fig. 5. Results of non-metric multi-dimensional scaling (MDS) analyses for A) each station averaged across all dates (stress = 0.01), and B) Stations A,B,C,E, and F for summer and winter samples (stress = 0.05).

ation across stations that was over 50% greater than that for deposit feeders ($P<0.001$; $t_6 = 9.68$, paired t-test).

Musculista senhousia

The number of recognized exotic species found in these samples is relatively low, but include a Japanese clam (*Theora lubrica* Gould) and a Mediterranean mussel (*Mytilus galloprovincialis* Lamarck). However, this count is certainly an underestimate due to limits of taxonomic resolution and the relatively poor characterization of marine invaders within the Californian biogeographic province (Crooks 1998a). Within the last 15 years, one exotic species, the mussel *Musculista senhousia,* has come to dominate the back of Mission Bay. Densities of the mussel reached a peak around 1988, dropped off dramatically over the following three years, and have subsequently increased again in the 1990's (Fig. 3).

Musculista senhousia in the subtidal of Mission Bay is short-lived and fast-

Table 2. Average dissimilarities of communities in the summer and winter samples. Also shown are the three species that contribute most to the differences in communities, as well as their contribution to the total dissimilarity (from SIMPER analyses).

Stations	Summer	Winter
A vs. B	Dissimilarity = 86%	Dissimilarity = 70%
	Musculista senhousia (32%)	*Phoronis* sp. (17%)
	Lumbrineris sp. (15%)	*Lumbrineris* sp. (16%)
	Praxillella pacifica (10%)	*Diplocirrus* sp. (12%)
A vs. E	Dissimilarity = 93%	Dissimilarity = 92%
	Musculista senhousia (23%)	*Lumbrineris* sp. (33%)
	Lumbrineris sp. (20%)	*Diplocirrus* sp. (17%)
	Praxillella pacifica (10%)	*Praxillella pacifica* (8%)
B vs. E	Dissimilarity = 76%	Dissimilarity = 90%
	Musculista senhousia (49%)	*Lumbrineris* sp. (18%)
	Neanthes arenaceodentata (10%)	*Phoronis* sp. (18%)
	Lumbrineris sp. (8%)	*Euchone* sp. (13%)

growing; the size-frequency histograms of *M. senhousia* display unimodal or bimodal distributions, suggesting the presence of only one or two year classes at any given time (Fig. 6). Modal sizes of mussels can change rapidly. For example, in January of 1983 there was a unimodal peak at 21.5 mm, with few small individuals present. Eight months later, the modal size of that cohort was 25.5 mm, and another cohort is evident with a mode of 15.5 mm. Four months later, the modal size of this second cohort was 21.5 mm. Growth in 1992 was less rapid, as the modal size did not change from January to June. The mean size of individuals, however, increased by 5 mm. There appears to be considerable variability of recruitment events of the population. Generally, the mean size of individuals is smaller in August and September, and larger in January and February.

To investigate relationships between the abundance of *M. senhousia* and species richness and total macrofaunal densities, regressions were performed on means of each station (excluding Station A, as the mussel was rarely found at this site) across all years (Fig. 7). Despite the increased dominance of *M. senhousia* in the bay, neither relationship was negative. There is no significant relationship between density of all other organisms combined and density of *M. senhousia* (Fig. 7A), and there is a significant positive relationship between number of other species present at a station and the density of the mussel (Fig. 7B).

Since *M. senhousia* is most abundant at Station B, and this station has been sampled on 21 dates between 1970 and 1996, it is possible to investigate longer-terms patterns that may emerge in relation to the increased abundance of this invader. Since 1970, there is no evidence of reduction in density or species richness at the station (Fig. 8A). The abundant invertebrate macrofaunal organisms (e.g., *Lumbrineris* sp., and *Diplocirrus* sp., and *E. limnicola*) present in the early stages of invasion by this mussel were still present in 1996, although there were negative correlations (across all stations from 1977–1996) for both *Diplocirrus* sp. and *E. limnicola.* There is also a possible negative relationship between the mussel and the deep-dwelling bivalve *Solen rostiformis* Dunker (= *S. rosaceus*), which was identified as a dominant at this station in the early studies (Dexter

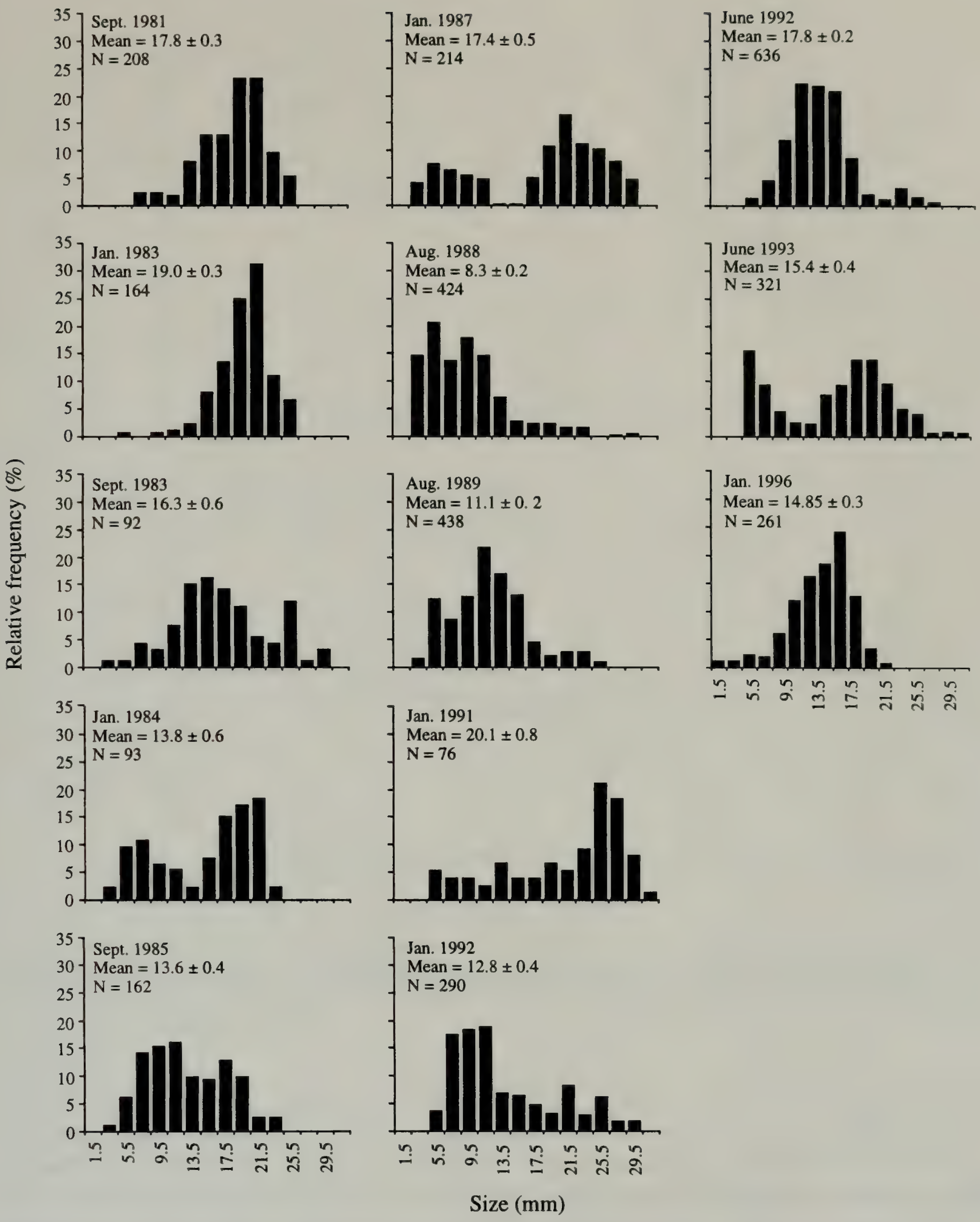

Fig. 6. Length-frequency distribution of *Musculista senhousia*. N = number of mussels measured. Mean sizes (± 1 s.e.) also are shown.

1983). Its average density between 1970 and 1987 (294 individuals collected) was 40/m^2, but had declined to 2.5/m^2 between 1988 and 1996 (6 individuals collected). One obvious change that has occurred is a shift from a primarily deposit-feeding community prior to 1980 (7 of 8 dates) to a suspension-feeding community thereafter (10 of 13 dates), which is due to the increased dominance of the suspension-feeding *M. senhousia* (Fig. 8B).

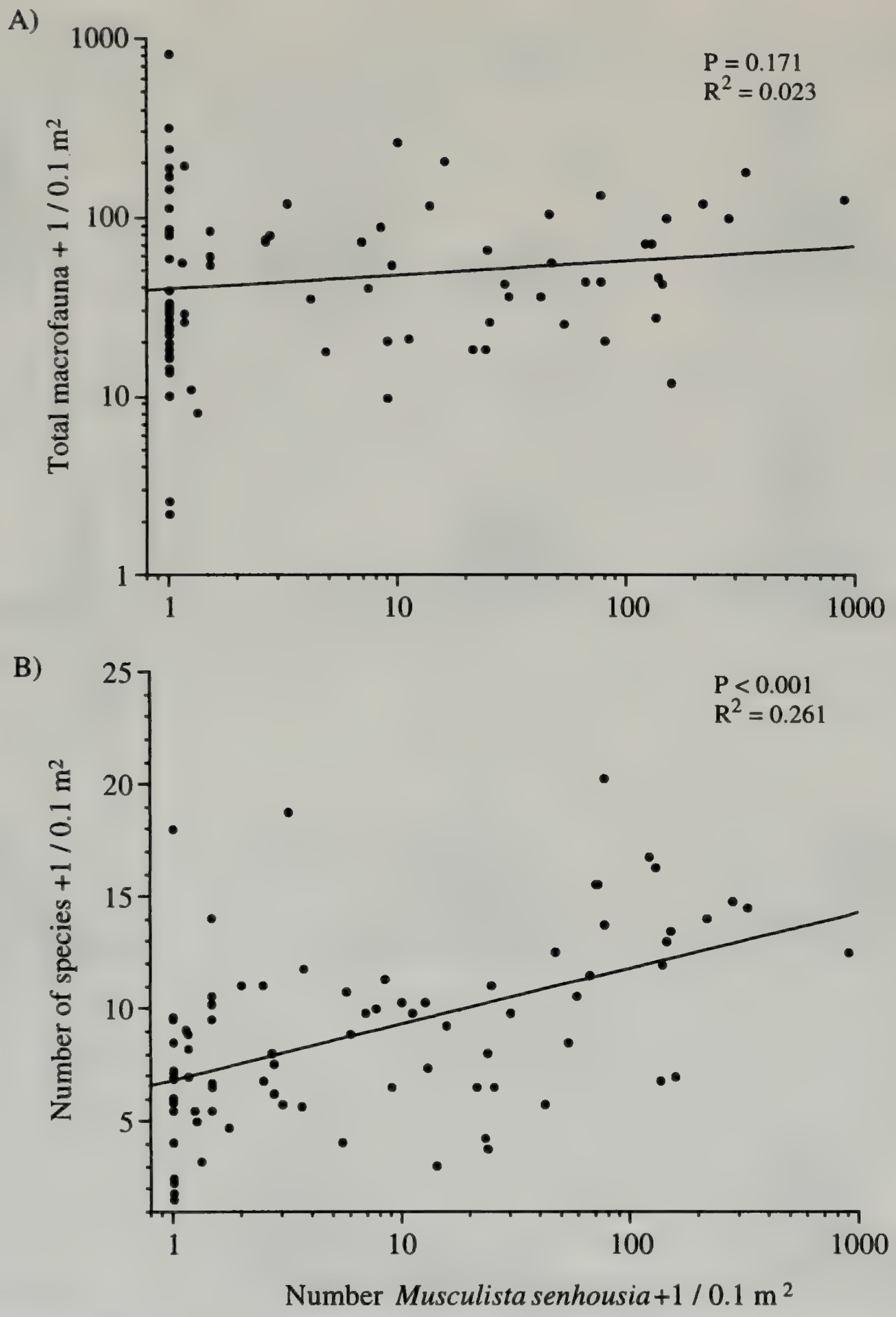

Fig. 7. *Musculista senhousia* vs. A) total number of individuals and B) total number of species. Data points are station means (excluding Station A). Calculations of total macrofaunal densities and species richnesses exclude *Musculista senhousia.*

Discussion

Within Mission Bay, there are distinct differences in community structure which appear to arise from gradients in the physical properties in the bay. Although Mission Bay is a lagoon with limited freshwater input and salinities often close to full seawater, salinity in the back bay is most variable and after heavy rain can be as low as 10 ppt (Levin 1982). Urban runoff, which is the primary source of freshwater in the system, is rich in organic matter (e.g. yard waste and leaf litter). Because the sources of runoff in this system are concentrated in the poorly-flushed areas of the back bay, conditions in this area are often considered degraded due to organic enrichment (San Diego Water Utilities Department 1978; Marcus 1989). Locations closer to the mouth of the bay, however, receive greater tidal flushing and are further away from the principal sources of runoff. This pattern of flushing and organic input likely have effects on sedimentary properties comparable to those reported in other systems (Pearson and Rosenberg 1978). Although quantitative sediment data for Mission Bay are limited, recent data are

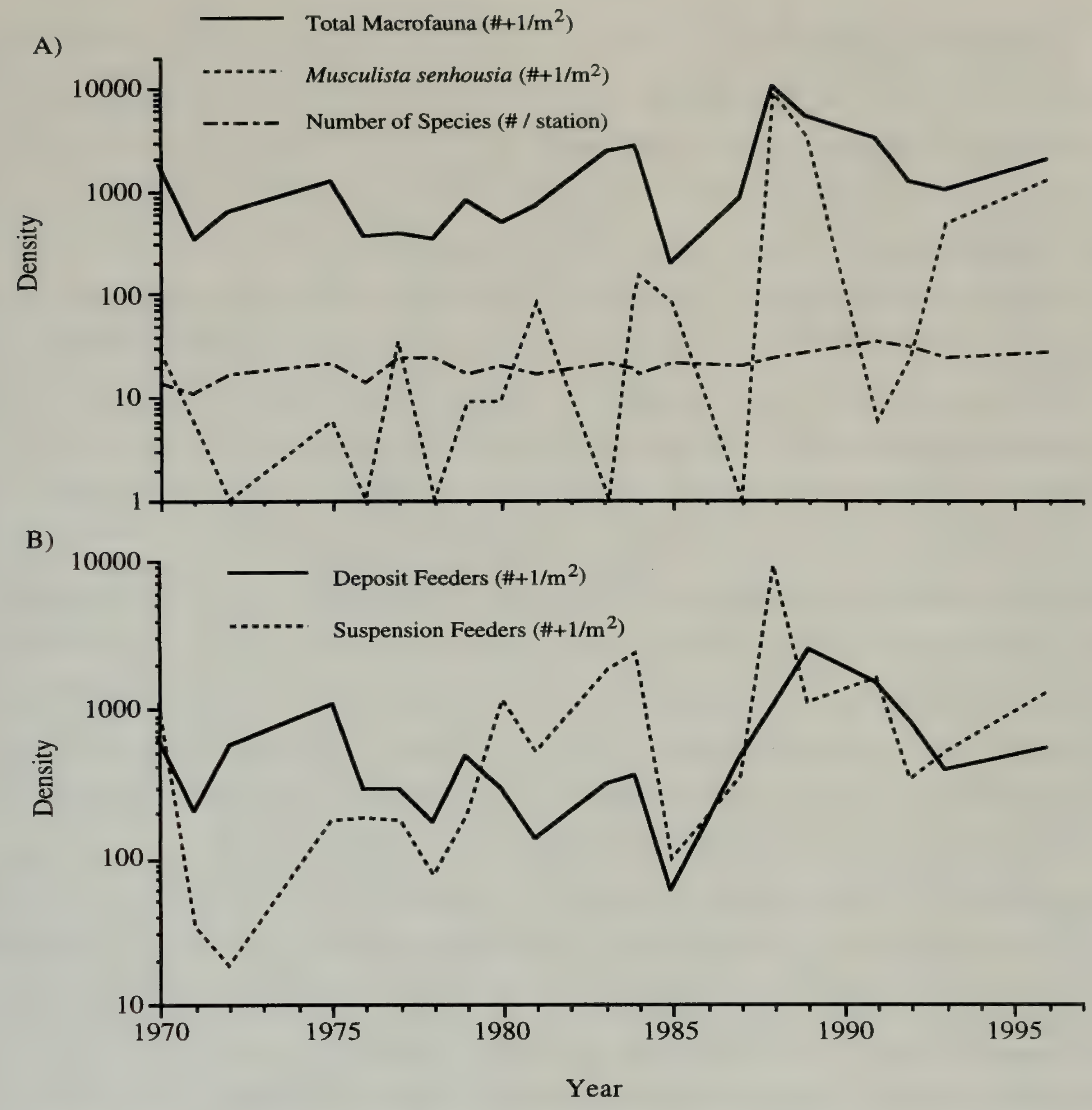

Fig. 8. Station B from 1970–1996. A) Average total densities (number m^{-2}), total number of *Musculista senhousia* (number m^{-2}), and species richness (number per station). B) Average densities of suspension and deposit feeders

characteristic of the reported flushing regimes (Fairey et al. 1997). In the back bay, combustible organic matter is high (2.5–2.6%) and sediment grain sizes are small (78–93% fine sediments < 63μm). Nearer the entrance of the bay, there is less organic matter (0.61%) and grain sizes are larger (33% fines) (Fairey et al. 1997).

Gradients in physical conditions such as those reported in Mission Bay can affect benthic assemblages, and organic enrichment (both natural and anthropogenic) are particularly important in structuring these communities (Pearson and Rosenberg 1978; Long and Chapman 1985; Jensen 1986; Brown et al. 1987; Friligos and Zenetos 1988; Heip 1995). Typically, communities in areas with low flushing and sources of organic input have low diversities and are dominated by opportunistic species (Pearson and Rosenberg 1978; Weston 1990). Such characteristics are found at Station E (nearest the mouth of Tecolote Creek), where species richness is low and the fauna is dominated by the exotic *Musculista senhousia* (Table 1; Fig. 3). Nearer the front of the bay, species richnesses increase as organisms that are absent or rare in the back bay become more common (e.g. *E. limnicola* and *P. pacifica*; Fig.'s 2 and 3). Total abundance and biomass both exhibit sharp peaks at Station B, which can be accounted for by the very high abundances of large-bodied *M. senhousia* in this area (Table 1; Fig. 3). The abundance of this invader drops dramatically nearer the mouth (Station A), even though known sedimentary properties from the area (Fairey et al. 1997) are within the reported range for the species (Crooks 1992, 1998b).

Feeding modes of species within estuarine systems also are reported to respond to environmental gradients, with deposit feeders replacing suspension feeding in areas of low flushing and finer sediments (Sanders 1958; Franz 1976; Pearson and Rosenberg 1978). However, this generalization has been questioned (Snelgrove and Butman 1994), and this pattern does not currently hold in Mission Bay. Station A, closest to the mouth, is typically dominated by deposit feeders (Fig. 4). In an earlier study of Mission Bay, Dexter (1983) found that the finer-sediment locations near the back bay (including Station B) also typically were characterized by deposit feeders (although occasionally suspension feeders such as *E. limnicola* and *Phoronis* sp. were abundant). However, *M. senhousia,* which has the ability to achieve high abundances in fine sediments (Morton 1974), has changed the representation of feeding modes near the back bay and created a community dominated by suspension feeders (Fig. 8). Another reported pattern related to feeding modes, that of greater variability in suspension- than deposit-feeding populations (Levinton 1972) was observed in Mission Bay (Fig. 4).

One striking feature of the faunal composition in the bay is the increased dominance by the mussel *M. senhousia* (Figs. 3 and 8). *Musculista senhousia* is well suited as an estuarine invader. It has anatomical adaptations to living in and processing fine sediments, broad temperature tolerances, and plastic habitat requirements (Morton 1974; Crooks 1992, 1996). It also is known to tolerate some degree of organic enrichment (Tsutsumi et al. 1991). *Musculista senhousia* has life-history characteristics typical of classic weedy, invasive species, as has been observed in this study and in shorter-term studies in the intertidal of Mission Bay (Crooks 1996) and in Asia (George and Nair 1974; Morton 1974; Tanaka and Kikuchi 1978). The species is short-lived (maximum of 2 years) and fast-growing, attaining sizes of 25 mm within 1 year. The mussel also has flexible reproduction and recruitment periodicity (Crooks 1996 and references therein) and temporally variable population densities (Fig. 3).

The potential effects of this invader are varied. Despite its ability to dramatically alter benthic habitats through the construction of dense byssal mats, a variety of small macrofauna often exist in higher abundances in the presence of the mussel. In the intertidal of Mission Bay, species richness, total macrofaunal densities, and densities of taxa such as crustaceans, small gastropods, and insect larvae are higher within mussel mats (Crooks 1998b). Similar increased densities or species richnesses of small macrofauna also have been reported in Hong Kong (Hutchings and Wells 1992) and New Zealand (Creese et al. 1997), and are related to the structural complexity and biogenic habitat provided by mussel mats (Crooks 1998b; Crooks and Khim 1999). In this study, the positive relationship between species richness and abundance of *M. senhousia* (Fig. 7B) suggests a positive effect of the mussel, although this also could be accounted for by similar responses of *M. senhousia* and other species to environmental conditions. Nonetheless, no negative effects on either species richness or total densities were detectable (Fig. 7).

Although positive effects of this species are common at one scale, animals not able to live within the matrix of the mussel mat may be negatively affected. Descriptive studies of bivalve abundances, as well as laboratory and field experiments, demonstrate negative effects of the mussel on abundance, growth, and survivorship of native clams (Sugawara et al. 1961; Anonymous 1965; Uchida 1965; Willan 1987; Crooks 1992; Creese et al. 1997; Crooks 1998a). Thick mats of *M. senhousia* also can inhibit vegetative propagation of the eelgrass *Zostera marina* L. (Reusch and Williams 1998). In the present study, bivalves with which *M. senhousia* may interact (such as *Solen rostiformis, Tagelus californianus* (Conrad), or *Laevicardium substriatum* (Conrad)) were not sufficiently abundant to document negative correlations. However, there has been a substantial decrease in the *Solen rostiformis* in the same time frame as the increase of *M. senhousia.* In addition, negative correlations were reported between *M. senhousia* and the polychaetes *E. limnicola* and *Diplocirrus* sp. One possible explanation for this is that both these polychaetes live in tubes which protrude above the sediment surface, and could thus be negatively impacted by the dense byssal mats of *M. senhousia.* Similarly, densities of the intertidal, tube-building polychaete *Pseudopolydora paucibranchiata* Okuda were lower in experimental plots containing artificial mussel mats (Crooks and Khim 1999). However, this tube-builder was not found in lower abundances within natural, intertidal mussel mats (Crooks 1998). Experimental manipulations would be necessary to further evaluate the relative importance of competitive interactions and responses to environmental factors (both natural and anthropogenic) in shaping these benthic communities.

The distribution of *M. senhousia* within Mission Bay, with decreased densities towards the mouth (Fig. 3), appears to be a general pattern that can be observed with exotics in other systems. For example, in San Francisco Bay the numbers of exotic species and their respective densities tend to increase dramatically towards the back of the bay (Carlton 1979; Hopkins 1986; Nichols and Pamatmat 1988). Such patterns seem to fit a positive relationship between a decline in habitat quality (as is often seen in back-bay locations) and the abundance of exotic species (Elton 1958; Orians 1986; Hobbs 1989; Pysek 1993; Kowarik 1995). However, this pattern is confounded by the fact that most transport mechanisms for estuarine exotics (e.g. ballast water movement, oyster transplantation, and ship fouling) are from one bay to another and bias against moving species adapted to open-ocean conditions (Carlton 1979; Ruiz et al. 1997). It is therefore difficult to quantitatively distinguish the role of habitat quality from that of vectors of introduction in determining invasibility of estuarine ecosystems. Nonetheless, it is clear that the rate of introductions within these areas is rapidly rising (Cohen and Carlton 1998; Crooks 1998a), and that exotic species will become increasingly important in shaping biotic communities within urbanized coastal ecosystems.

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Investigations of Red Tides Along the Southern California Coast

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Abstract.—Prior to 1976 red tides of the dinoflagellate *Lingulodinium polyedra* usually developed during the fall of the year. From 1976 until 1994 there was an hiatus of red tide blooms. In the winter of 1995 an extensive red tide, dominated by *L. polyedra,* developed along the entire Southern California Bight. This new pattern of winter and spring red tides continued through 1996 and 1997. In addition, a localized red tide persisted at the Los Angeles River mouth from winter through summer. During post-bloom conditions, *L. polyedra* cells were observed erupting from their cell walls, taking on a naked amoeboid form.

Algal blooms are called red tides when the cell densities are high enough to change water color, often to red. Such blooms have long been a common phenomenon within the Southern California Bight (SCB), with the earliest reported red tide occurring in 1746 (Brongersma-Sanders 1957). Red tides can occur in nearly any month of the year and are generally more prominent in nearshore waters (Oguri *et al.* 1975). Many reported red tides in the past were accompanied with observed mortality of fish and shellfish, while others resulted in no reported damage to the marine system.

The specific causes and oceanographic conditions which set the stage for red tides are not completely known (Hardy 1993). Nutrients levels, water temperature, light availability, and zooplankton grazing are all involved in the determination of phytoplankton doubling rates. If these factors are optimized, rapid growth of one or several species can lead to natural blooms. In addition, nutrient enrichment due to agricultural runoff, urban storm drain runoff, sewage effluent and general inshore eutrophication can lead to enhanced algal growth.

In the past, the dominant organisms responsible for red tides in the SCB have been the dinoflagellates *Prorocentrum micans* and *Gonyaulax polyedra,* and mortality of fish and invertebrates have been associated with red water of the latter (Brongersma-Sanders 1957). Spring blooms were usually associated with *P. micans,* while the more intensive red tides of the late summer and fall were commonly dominated by *G. polyedra* (Sweeney 1975). In 1967 Goodman *et al.* (1984) identified three distinct phytoplankton communities, two of which were dominated by diatoms and associated with upwelling conditions, and the third dominated by *Gonyaulax polyedra.* This *Gonyaulax* dominated community was correlated with a shallow pigment layer, low silicate, and high temperatures. This condition is the one usually correlated with red tide formation during the summer and fall months.

The pattern of bloom development in the SCB has shown marked variations during the past several decades. Prior to 1975, blooms of the dinoflagellate *Gonyaulax polyedra* usually developed during the fall of the year. The triggering

Table 1. *Lingulodinium polyedra* (*Gonyaulax polyedra*) red tides off southern California 1901–1977 (Data from 1901 to 1962 from Brongersma-Sanders 1957, and Oguri 1964).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1901							Torry (1902) mortality					
1907								Kofoid (1911) mortality				
1917									Allen (1921) mortality			
1938					Allen (1938)	Allen (1938)						
1945									Pope (1946) mortality	Allen (1946)		
1952							Brongersma (1957)					
1962										Oguri (1964)		
1975								Pieper (unpubl.)				
1976												
1977							Gaines (1981)			Gaines (1981)		

mechanism(s) for these blooms are unknown but natural causes are usually invoked. Stratified conditions due to the lack of mixing or dispersion, coupled with nutrient availability, possibly from coastal upwelling, may have provided the setting needed for maximum dinoflagellate growth and aggregation. A seed population would have been needed for these blooms to develop. This seed population may have been present in the plankton in small numbers, or may have arisen from benthic cysts. These blooms failed to continue into the late fall and winter, presumably as light became limiting and storms mixed the water column. This seemingly stable pattern culminated in the fall of 1975 when the area experienced a bight-wide bloom.

Then, from 1975 until 1994 there was a hiatus of red tide blooms, except for localized red tides in Los Angeles Harbor in 1976 and 1977 (Morey-Gaines 1981). See Table 1 for a summary of red tide blooms of *Gonyaulax polyedra. Gonyaulax polyedra* was reclassified as *Lingulodinium polyedra* by Dodge (1989). Although Steidinger and Tangen (1997) refer to *Lingulodinium polyedra* as *Lingulodinium polyedrum,* it will be referred to as *Lingulodinium polyedra* henceforth.

The pattern again changed abruptly in 1995 when an extremely large precipitation event occured early in January of 1995, followed by Santa Ana wind conditions (warm, dry, sunny). Concurrent with this meteorological sequence an extensive red tide condition developed along the entire coast of the SCB. This large scale bloom persisted from January through April, and was recorded from Santa Barbara to San Diego, and offshore as far as San Clemente Island. Cell concentrations were measured at La Jolla in excess of 2 million cells 1^{-1} (Hayward *et al* 1995). In the vicinity of Los Angeles Harbor the red tide peaked and crashed on March 11, leaving dissolved oxygen levels of 3.5 mg/l. This depressed dissolved oxygen concentration is lower than the minimum regulatory objective of 5.0 mg/l for the Los Angeles and Long Beach Harbors complex as determined by the California Regional Water Quality Control Board.

Analysis performed by the California Department of Health Services in March of 1995 determined that *Lingulodinium polyedra* was the dominant dinoflagellate in the bightwide red tide. Sporadic localized red tides persisted through the spring of 1995, including a red tide condition stretching from the Los Angeles River mouth eastward to Belmont Pier, Long Beach. Continued sampling by the authors during this period confirmed that these subsequent smaller red tides were also dominated by *Lingulodinium.* Other dinoflagellate genera present in the mainland coastal samples included *Prorocentrum, Protoperidinium,* and *Ceratium.* Immediately following the crash of the bightwide red tide event, naked dinoflagellate cells were observed in plankton samples. These naked dinoflagellates were suspected to be an unarmored form of *Lingulodinium.*

Smith (1995) has proposed 1985 as a boundary year in terms of oceanographic conditions in the southern California Bight. Between 1985 and 1994 sardine larvae and sea surface temperatures have increased, while small plankton volume and anchovy larvae have decreased. The ecological system of the Southern California Bight appears to have undergone some significant change, and this change may have included a shift in dinoflagellate bloom seasonality.

These initial observations from early 1995 indicated more than just a shift in the seasonality of red tide blooms. Enrichment from urban runoff may have played a role in the bightwide red tide of 1995. Red tide conditions also persisted at the mouth of the Los Angeles River after the collapse of the bightwide red tide. The Los Angeles River is a major flood control channel for urban runoff. In addition, it receives a large component of its flow from sewage treatment plants. Field and laboratory studies were initiated to further investigate these red tide phenomena.

Methods

From Spring 1995 through Spring 1997 field measurements and samples were performed from ships of opportunity. Vertical plankton tows, to a depth of 10 meters, were performed using a phytoplankton net, 20 cm. in diameter and 1 meter long, with 80 micron mesh. Plankton was sampled at three locations: (a) the mouth of the Los Angeles River, located within the Los Angeles/Long Beach Harbor complex; (b) one mile outside of the Los Angeles Harbor breakwater; and (c) oceanic water near Bird Rock on the north side of Santa Catalina Island. Samples were analyzed at the Fish Harbor Laboratory for relative dinoflagellate population densities (by genus, given in percent of total dinoflagellates). Naked dinoflagellates were assigned their own category and were not identified to genus. Cell counts of diatoms were also performed for each sample to determine relative concentrations of diatoms to dinoflagellates. In addition, a count of zooplankton, excluding protozoans, was performed for each sample to determine the relative abundance of phytoplankton to zooplankton.

During the same period several Secchi disc and Forel Ule color measurements were performed at the mouth of the Los Angeles River and outside the Los

Angeles Harbor Breakwater to produce indicators of water transparency and relative color. The light extinction (k) was calculated from the Secchi depth using the equation $k = 1.7 / d$, where d is the Secchi depth in meters (Raymont 1963). Nutrient analyses, for ammonia nitrogen, nitrate nitrogen, and orthophosphates were performed on samples collected at the mouth of the Los Angeles River from Spring 1995 through Summer 1996. Ammonia nitrogen was measured using the Salycilate Method (Reardon *et al* 1966). Nitrate nitrogen was determined using a modified Cadmium Reduction Method (modification of Eaton *et al,* Standard Method 4500-NO_3-E 1995). Orthophosphates were tested using the Ascorbic Acid Method (modification of Eaton *et al,* Standard Method 4500-PE 1995). All results were read colorimetrically.

Laboratory pure cultures of *Lingulodinium polyedra* and *Prorocentrum micans* were originally collected from southern California waters in the 1960's and maintained since then by the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP), located at the Bigelow Lab for Ocean Sciences in West Boothbay Harbor, Maine. Sub-cultures were transported from CCMP to SCMI's Fish Harbor Lab in 1995, then subjected to a series of assays to investigate some simple environmental parameters.

Culture light conditions included a 12 hour photoperiod with broad spectrum cool white fluorescent lighting, 80 microeinstein intensity. For each experiment there were 5 replicates of each species in 40 ml screw top test tubes, 25 mm diameter, placed in racks with even access to light. The caps were left loose to allow diffusion of air into the tubes. The caps were tightened and the tubes inverted on a daily basis. The stock culture media consisted of f/2 in sterile seawater. The seawater source was the Fish Harbor Laboratory seawater system. The seawater was filtered through a 5 micron filter, f/2 added, and then autoclaved prior to use.

Test cultures were inoculated from the stock culture of each species at the curve of optimum population growth. Cultures were inoculated by adding 50 ml of media per 10 ml of culture. The cultures for each variable and control replicate are derived from the same well mixed test tube. Control culture media was the same as for the stock cultures (i.e., f/2 in sterile Fish Harbor water). Cell counts are measured at the beginning of the experiment and at regular intervals throughout the experiments.

Results

Field Studies

Extensive red tides were not observed during the summer and fall of 1995, except at the mouth of the Los Angeles River. Following the winter rains in 1996, patchy red tides developed in San Pedro Bay, both inside and outside of the harbor. One red tide occurred in late February and early March, and was dominated by *Ceratium.* Another red tide developed in late March and lasted into early May, and was dominated by *Lingulodinium.* Following winter rains in 1997 and a spring characterized by relatively high winds, a red tide once again developed throughout San Pedro Bay during early May. This red tide was reported in Santa Monica Bay as well (T. Tamminen, personal communication). This red tide was dominated by *Lingulodinium* and culminated in a crash on May 10, 1997. See Table 2 for a summary of *Lingulodinium* red tide observations from 1995–1997.

Aside from the wide-spread red tides, a localized red tide persisted at the mouth of the Los Angeles River during 1995 and 1996, from winter through summer months. These red tides were sometimes observed to extend eastward for as much as two miles along the Long Beach coastline. Regular plankton sampling at the Los Angeles River mouth was not conducted in 1997; however, the red tide of May 1997 in San Pedro Bay was observed and sampled at the Los Angeles River mouth.

Nutrients were generally abundant at the Los Angeles River mouth, although values varied considerably between samples (see Table 3). For the study period mean ammonia nitrogen was 15.4 μg-atoms/L, mean nitrate nitrogen was 24.8 μg-atoms/L, and mean inorganic phosphorus was 2.6 μg-atoms/L. As expected, the concentrations were greater during the winter rainy season.

Measurements of the coefficient of light extinction (k) at the river mouth yielded results between 0.57 and 3.4. Outside of the harbor the k values were lower (i.e., the water was less turbid), between 0.16 and 0.49 (Figure 1). At the river mouth, the Forel Ule scale readings were between XII and XVIII (i.e., ranging from yellow to red). Outside of the harbor the Forel Ule color results were between III and X (i.e., generally blue-green to green; Figure 2).

Armored *Lingulodinium* was the most abundant dinoflagellate taxa in a majority of the samples, regardless of location. At the river mouth armored *Lingulodinium* was the dominant dinoflagellate, followed by naked dinoflagellates. When counts from all samples at this location were combined, 48% of all dinoflagellate cells were armored *Lingulodinium,* and 28% were naked dinoflagellate cells (Figure 3). Throughout the study the two most common of the naked cells were identified as *Gymnodinium* and an amoeboid cell hypothesized to be a life stage of *Lingulodinium.* In many of these samples, the dominant naked cells were of the latter form. During the crash of the May 1997 red tide, samples were observed, from the Los Angeles River mouth as well as other locations, with naked cells erupting from *Lingulodinium* thecae. This confirmed that the naked cells in the May 1997 samples were in fact *Lingulodinium.* This also gave more credence to the idea that some of the naked cells observed in previous samples, both at the river mouth and elsewhere, may also have been an amoeboid life stage of *Lingulodinium.* This phenomena was videotaped, using light microscopy, and digitized into still micrographs (Figure 4).

Outside of the harbor breakwater, armored *Lingulodinium* was again the dominant dinoflagellate. For all samples at this location combined, 45% of all dinoflagellate cells were armored *Lingulodinium,* 22% were *Ceratium,* and 16% were naked dinoflagellate cells (Figure 3). For all samples at Catalina combined, armored *Lingulodinium* represented 31% of all dinoflagellate cells, 26% were *Ceratium,* and 24% were naked dinoflagellate cells.

The ratio of phytoplankton to zooplankton was noticeably different at these sampling stations. Generally, the phytoplankton to zooplankton ratios decreased with distance from the river mouth out to less impacted offshore waters. At the river mouth, the median was 1425:1, immediately outside of the harbor the median was 503:1, and at Catalina the median was only 159:1. At the river mouth, only 22% of the samples had phytoplankton to zooplankton ratios of less than 999:1;

Table 2. *Lingulodinium polyedra* (*Gonyaulax polyedra*), red tides off Southern California, 1995–1996. (LA = Los Angeles; SM = Santa Monica; MDR = Marina Del Rey; Platforms are located in the outer portion of San Pedro Bay; Offshore refers to the San Pedro Channel out to Santa Catalina Island).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1995	La Jolla	SM Bay	Fish Harb MDR	Belmont	LA River							
1996	LA River	LA River	LA River Fish Harb Platforms SM Bay	LA River Fish Harb Offshore SM Bay MDR	LA River Fish Harb Offshore	LA River	LA River					
1997					Santa Monica Bay Sand Pedro Bay, L.A. River							

Table 3. Nutrient concentrations, Los Angeles River mouth, all results in μg-at/l.

	Maximum measurement	Mean, rainy season	Standard dev., rainy season	Mean, dry season	Standard dev., dry season	Mean, study period	Stan. dev., study period
ammonia nitrogen	42.8	21.2	14.4	6.0	5.7	15.4	13.8
nitrate nitrogen	214.2	36.9	70.6	3.1	6.6	24.8	58.0
inorganic phosphorus	242.7	3.1	3.1	1.7	1.2	2.6	2.6

the remainder (78%) had ratios between 1,000:1 and 9,999:1. Immediately outside of the harbor, a majority of the samples, 74%, had a ratio of less than 999:1. At Catalina, 91% of all samples had phytoplankton to zooplankton ratios of less than 999:1 (see Table 4).

The ratios of dinoflagellates to diatoms were also noticeably different at the three sampling stations. Generally, there were decreasing ratios of dinoflagellates to diatoms from the eutrophic river mouth out to less impacted waters. At the river mouth, the median was 39:1, and 89% of the samples had a ratio of greater than 9 dinoflagellates per every 1 diatom. Immediately outside of the harbor the median was 17:1, with 59% of the samples having ratios greater than 9:1. At Catalina the median ratio of dinoflagellates to diatoms was only 6:1, and a majority (63%) of the samples had ratios less than 9:1 (see Table 5).

Laboratory Studies

Lingulodinium polyedra and *Prorocentrum micans,* the two dominant species in the 1995 red tide, were subjected to salinity assays. Test salinities were 15, 25 and 35 parts per thousand. Both cultures displayed a tolerance for depressed salinity levels. *L. polyedra* grew well in both 35 and 25 ppt salinity water, but perished at a lower salinity of 15 ppt (Figure 5). *P. micans* grew well at all three salinities of 35, 25, and 15 ppt. *P. micans* also grew at a faster rate than *L. polyedra* under identical water quality conditions (Figure 6). These results indicate that *P. micans* has an even higher tolerance to stressful water quality conditions (i.e., depressed salinity) than *L. polyedra.* This is not surprising, since *P. micans* is known as a euryhaline species, with its range of tolerance between 15 and 40 ppt, and an optimum salinity of 25 ppt (Kain and Fogg 1960).

Laboratory pure cultures of *L. polyedra* were also grown in water from the mouth of the Los Angeles River in two experiments. In one experiment these cultures were subjected to summer dry season (35 ppt) water quality, and in the other experiment the salinity was depressed (32 ppt) by the presence of winter storm water runoff. For both of these assays, reference cultures in f/2 nutrient

Table 4. Phytoplankton to zooplankton ratios. Categories represent ranges of ratios grouped by orders of magnitude. Values are percentages of all samples that fall into the respective categories.

Ranges of phytoplankton to zooplankton ratios	0.1–9	10–99	100–999	>1,000
L.A. River (% of samples)	0	22	0	78
Outside Harbor (% of samples)	0	5	69	26
S. Catalina Island (% of samples)	14	18	59	9

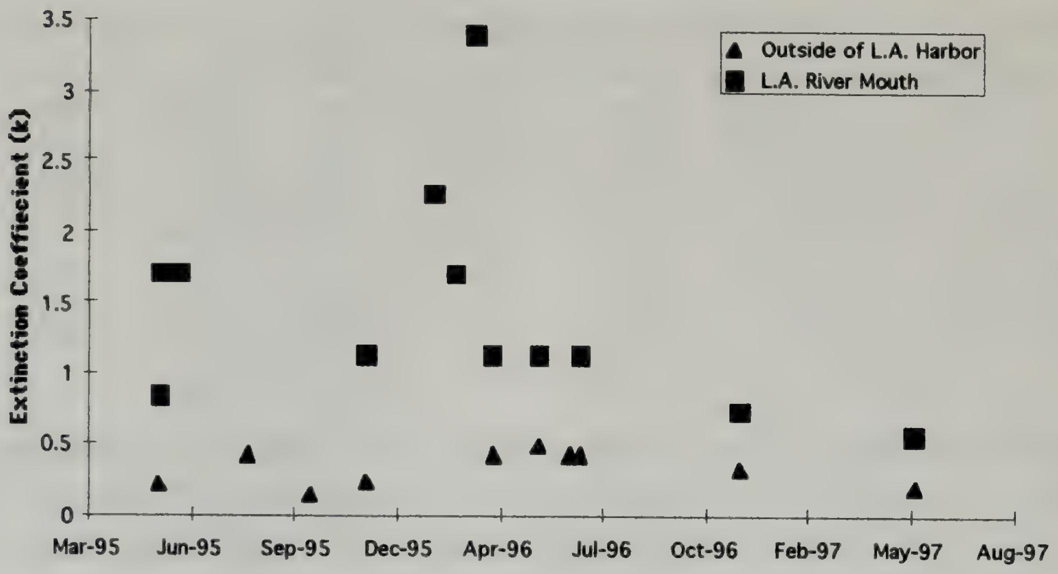

Fig. 1. Coefficient of light extinction (k) at the Los Angeles River mouth and outside of the Los Angeles Harbor breakwater.

media were maintained simultaneously to the test cultures. In the dry season experiment, *L. polyedra* did poorly, actually declining in population size. This may have been due to the absence of some limiting nutrient, or the presence of some toxicant in the river runoff. In the second experiment, evaluating the impact of storm water runoff conditions, *L. polyedra* experienced a 143 percent increase in population size in a 23 day period compared to a culture of *L. polyedra* grown in offshore water (from near Catalina Island) which had only a 12 percent increase (Figure 7).

Discussion

Red tide reports associated with the dinoflagellate *L. polyedra* (previously *Gonyaulax polyedra*) from 1901 through 1977 were from the summer and fall seasons. There were no reported red tides in the SCB from 1978 through 1994, a sixteen year period. Then, between 1995 and 1997 the red tide blooms of *Lingulodinium* in the Southern California Bight were observed during the late winter and spring periods of the year. This marked a major shift in the seasonality of

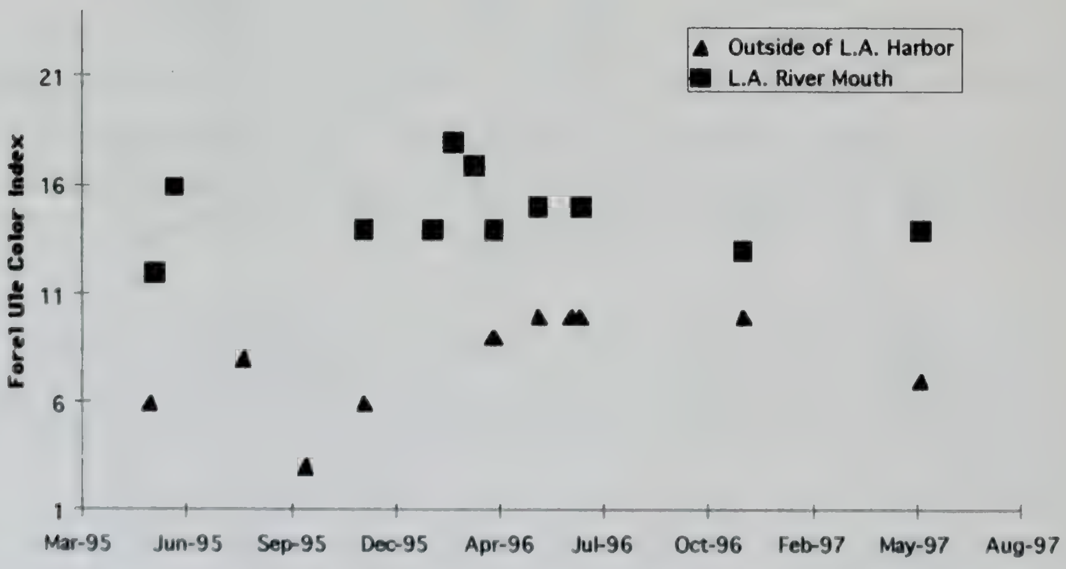

Fig. 2. Forel Ule Color at the Los Angeles River mouth and outside of the Los Angeles Harbor breakwater.

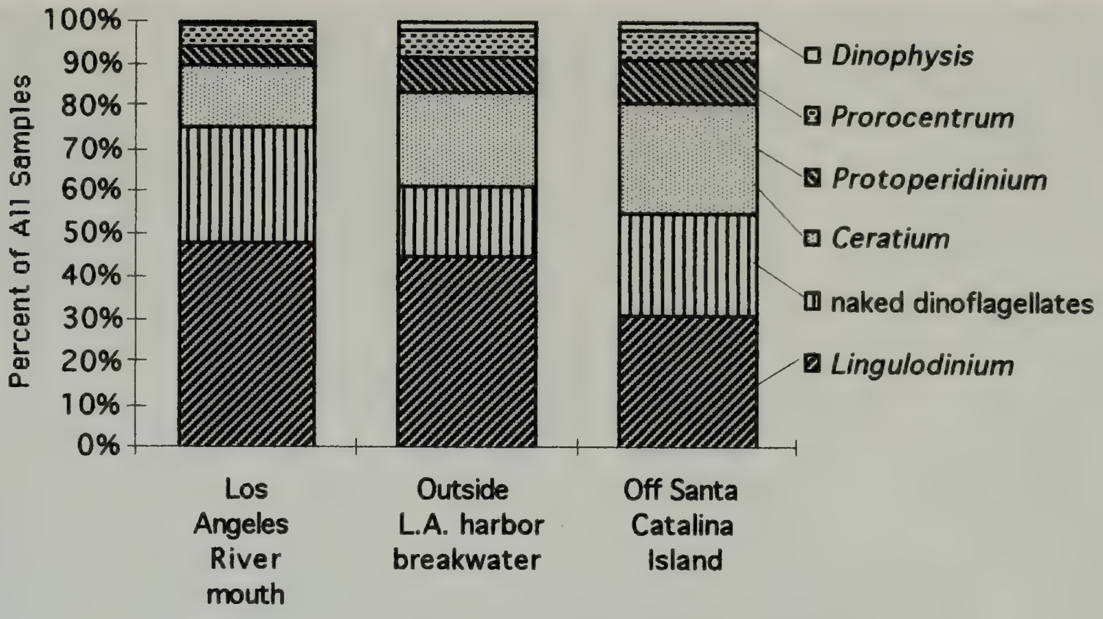

Fig. 3. Dinoflagellate community composition.

dinoflagellate blooms, which coincided with other significant changes in the ecological system of the Bight, such as increased temperature, decreased small plankton volume, and a shift in larval abundance from anchovy to sardines.

Beyond its coincidence with these other ecological changes, the ultimate reason for the change in the seasonal pattern of red tide development is not obvious. Even the causes of these bightwide red tides in general are still elusive. Potential causes may be related to wind and/or coastal runoff. The largest red tides during the years 1995 to 1997 followed windy periods. Wind blowing over the ocean can cause an increase in the mixed layer and/or coastal upwelling, thereby enriching the euphotic zone with nutrients. There is also some indication that river and storm drain output, providing abundant nitrogen (including the forms of ammonia or urea), may be an important stimulus for bloom formation. Available nitrogen is often the limiting macronutrient in marine systems, with ammonia and urea being the preferred forms for algal uptake. The present study shows that both *L. polyedra* and *P. micans* are tolerant of depressed salinities associated with river runoff. Coastal southern California experiences appreciable rain and associated runoff only during the winter season, and during the present study period large scale red tides only occurred during the winter and early spring periods. The higher nutrient availability in the runoff may be exploited by dinoflagellates because of the coincidental availability of organic complexing agents (i.e., humic acids) found in river and terrestrial runoff. These organic complexing agents bind with manganese and copper. Under offshore conditions (i.e., upwelling rather than runoff) manganese and copper result in mortality to dinoflagellates (Dempster 1955; Loeblich 1967; Anderson and Morel 1978). Organic complexing agents are suggested as important agents for the development of red tides (Prakash and Rashid 1968; Collier *et al.* 1969; Doig and Martin 1974).

The persistent, localized red tide condition at the Los Angeles River mouth is likely due to eutrophication resulting from urban runoff. Dinoflagellate blooms have been documented in other polluted, eutrophic water bodies along the east coast of the U.S., such as Chesapeake Bay, New York Bight, and Long Island Sound. These waters are characterized by having elevated ammonium:nitrate ra-

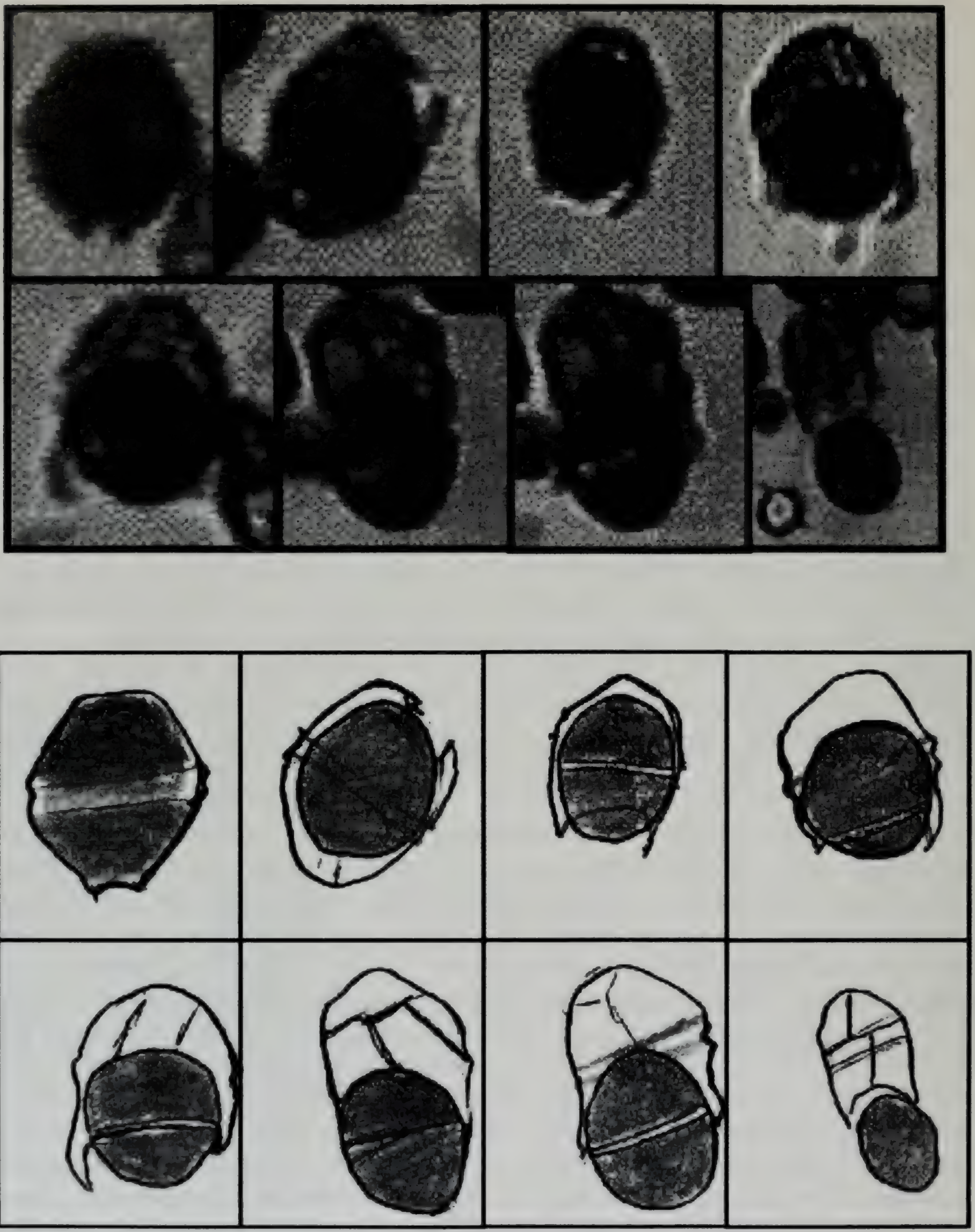

Fig. 4. Naked cells erupting from *Lingulodinium polyedra* thecae. The following series represents the emergence of amoeboid cells from intact *Lingulodinium polyedra.* Each frame is of a different cell, but from the same sample. The figure in the upper left shows an intact cell. The figure in the lower right shows the fully emerged amoeboid cell and the empty theca. Although all cells were the same size, some appear smaller due to the manipulation of the images to fit within these frames. The top panel is composed of digital photographs. The bottom panel is composed of line drawing interpretations of the digital photographs.

Table 5. Dinoflagellate to diatom ratios. Categories represent ranges of ratios grouped by orders of magnitude. Values are percentages of all samples that fall into the respective categories.

Ranges of phytoplankton to zooplankton ratios	0.1–9	10–99	100–999	1,000–9,999	>10,000
L.A. River (% of samples)	11	45	11	11	22
Outside Harbor (% of samples)	41	27	9	23	0
S. Catalina Isl. (% of samples)	63	5	32	0	0

tios and high concentrations of dissolved organic compounds (McCarthy *et al.* 1977; Paasche and Kristiansen 1982).

Within the study area, the Los Angeles River, flowing into the Los Angeles/Long Beach Harbor complex, contains sewage plant effluent throughout the year and significant urban storm drain runoff during the rainy season. Elevated nutrient levels during 1996 were measured in association with the winter and early spring peak runoff period. Runoff flows into the harbor where the lack of mixing is conducive to dinoflagellate bloom development. The dinoflagellates decrease in abundance, in relation to diatoms, with distance from the mainland harbor complex. The dinoflagellate community composition also changes with distance away from the harbor complex, with *Lingulodinium* occupying a less dominant role in the less impacted offshore water. This is further supported by the laboratory assays, in which *L. polyedra* cultures grew more favorably on wet season Los Angeles River mouth water as compared to cleaner offshore seawater.

The life history of *Lingulodinium,* in terms of its amoeboid stage, brings up interesting ecological questions. The amoeboid stage occurs during stressful post bloom conditions. It is possible that this stage has an adaptive advantage with regard to mobility or reproduction. Possibly the amoeboid stage is a better predator than the armored stage. There may also be a relationship between this stage and the benthic (dormant) cyst stage. The amoeboid stage may be more vulnerable to predation, unless this stage has built-in toxic safeguards that are as yet un-

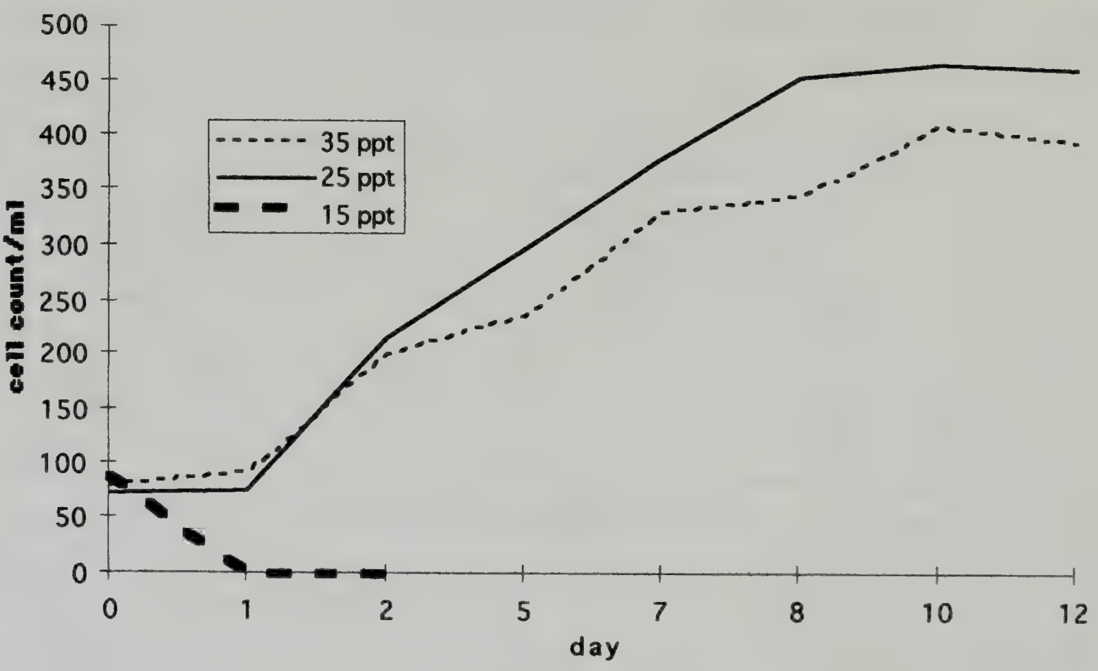

Fig. 5. *L. polyedra* response to three different salinities.

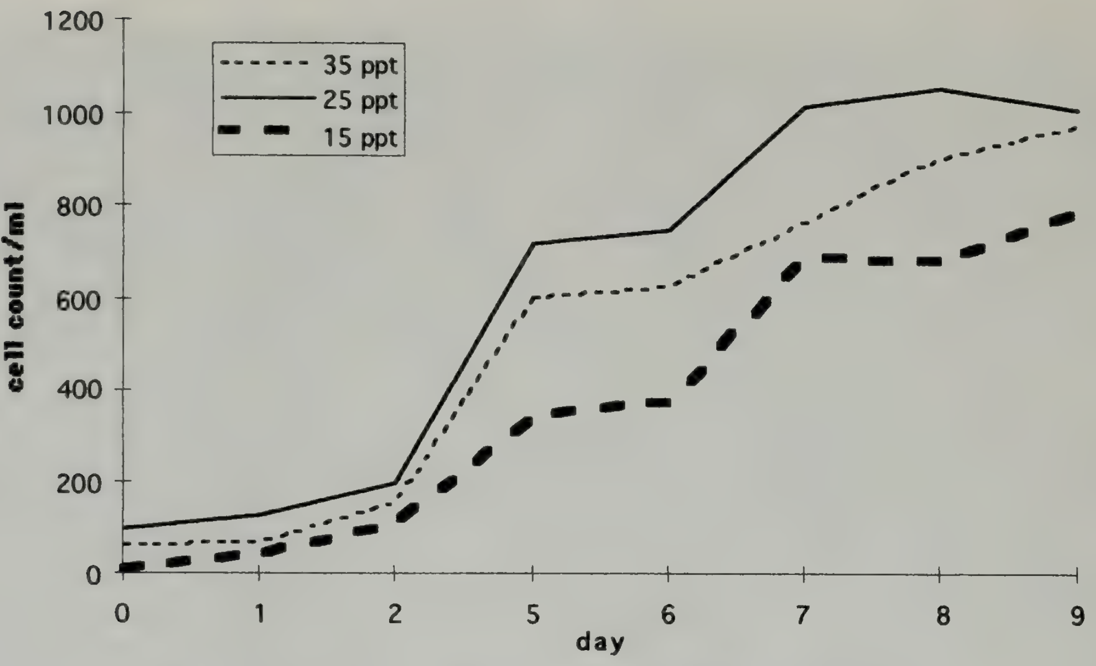

Fig. 6. *P. micans* response to three different salinities.

known. Possibly there are fewer zooplankton organisms in post bloom conditions, thereby reducing the risk of predation.

Past data on red tide events off southern California are, at best, sporadic. Many of these are largely a function of reports which originate only when investigators were in the field, rather than as a result of consistent sampling strategies. Similarly, the results reported herein were, due to budget constraints, largely obtained through the use of ships of opportunity. The occurrence of *Lingulodinium* red tides and other harmful algal blooms in the Southern California Bight deserves further study. A consistent field sampling plan and additional laboratory investigations are recommended to examine further the nature of red tides off southern California.

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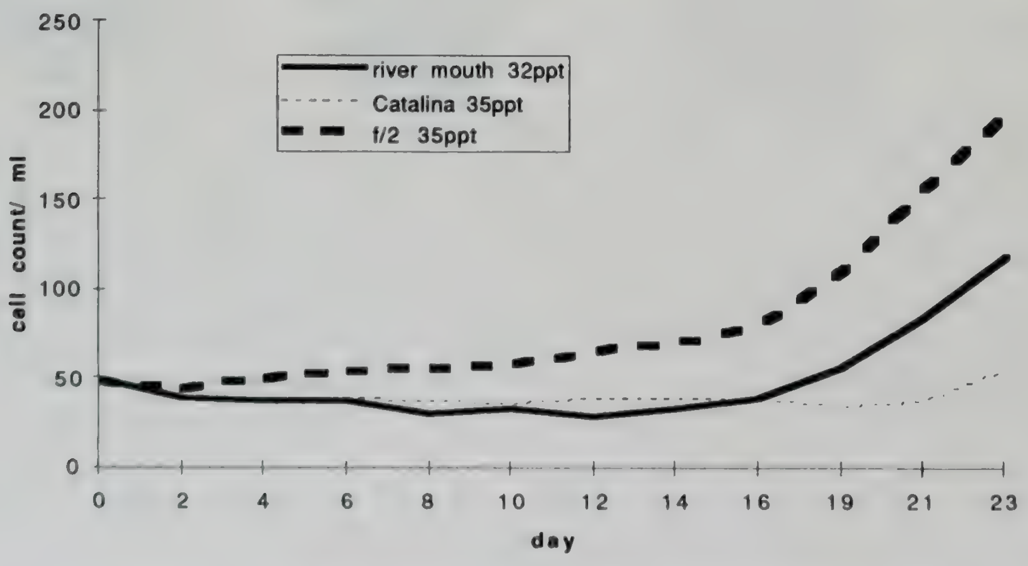

Fig. 7. *L. polyedra* response to urban runoff vs. offshore water and ideal culture media.

Table 6. *Lingulodinium polyedra* (*Gonyaulax polyedra*) red tides off Southern California.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1901							XX					
1907												
1917									XX XX			
1938					XX	XX						
1945									XX	XX		
1952							XX					
1962										XX		
1975								XX				
1976							XX					
1977										XX		
1995	XX	XX	XX	XX	XX							
1996	XX	XX	XX	XX	XX	XX	XX					
1997					XX							

vasoli-Guillard National Center for Culture of Marine Phytoplankton. Crystal Brandt, Matt Sullivan, and Carrie Wolfe of the Southern California Marine Institute also provided valuable assistance. Also, many thanks to Dr. Francis McCarthy and Bill Wilson for their helpful comments on this paper.

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The Influence of Bay versus Coastal Habitats on Development and Survival of Striped Shore Crab Larvae (*Pachygrapsus crassipes* Randall 1840)

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Abstract.—The striped shore crab, *Pachygrapsus crassipes,* lives in both protected embayments and exposed nearshore coastal habitats and larvae may develop in either setting. This study compared survivorship and development of *Pachygrapsus crassipes* zoeae brooded in two southern California embayments and an exposed coastal habitat and cultured in corresponding waters under laboratory conditions. Larvae cultured in nearshore coastal seawater experienced higher survivorship during zoeal development, exhibited a higher percentage of stage VI zoeae surviving to the post-larval megalopal stage, and yielded a larger percentage of viable megalopae than larvae reared in seawater collected from either San Diego Bay or Mission Bay. This study suggests that brood site and culture water source will influence *P. crassipes'* rate of development and survivorship.

The early life history of many nearshore benthic invertebrate species involves the release of planktonic larvae (meroplankton) that remain in the water column until ready to settle as juveniles or adults (reviewed by Levin & Bridges 1995). The planktonic phase provides a vehicle for larval dispersal, gene flow between populations, and colonization of new habitats (Thorson 1950; Mileikovsky 1971; Scheltema 1971). Larval dispersal strategies vary; some larvae are retained within estuaries, other species are preferentially exported to coastal waters (Epifanio 1988), while others are spawned offshore and must migrate onshore (reviewed by Shanks 1995).

The trade-off between nutrition, predation, and physiological stress have been offered as explanations for why certain larvae may be preferentially exported from estuaries while others are retained throughout their development. Estuaries are considered to be more productive than coastal waters (Ferguson *et al.* 1980) and may provide more food. However, the higher productivity of estuaries also supports more predators (Weinstein 1979) and certain taxa may favor reduced predation pressure associated with coastal waters (Morgan 1987a). Physiological stress is usually greater in estuaries due to larger temperature and salinity fluctuations depending on the size of embayments and freshwater input (Morgan 1987b).

Most studies that have addressed the adaptive significance of larval development in bays versus coastal waters have focused on species that inhabit bays as adults and show a clear preference for being exported to coastal waters or retained within embayments through larval development. However, a number of marine benthic invertebrate species inhabit both estuarine and exposed coastal habitats during larval and adult stages of development. Gaines and Bertness (1992) have shown for the Narragansett Bay region that acorn barnacle larvae, *Semibalanus balanoides,* develop and recruit within bay or coastal habitats and that rainfall-driven bay flushing largely controls the exchange of larvae between these habitats. Embayments and open coastal environments can differ considerably with respect to physical (light, temperature, salinity, flow), chemical (elemental contaminants), and biological (food availability, predation pressure) factors. Larvae that are brooded or released in these respective habitats may experience developmental differences that ultimately affect population success.

In southern California, adults and larvae of the striped shore crab, *Pachygrapsus crassipes,* are widely distributed in low-energy bay habitats and exposed coastal habitats. The majority of adult crabs found in embayments inhabit burrows built into the sides of tidal creeks in high intertidal marshes, while inhabitants of the high-energy rocky intertidal occupy predominantly high and mid-level crevices and tidepools (Hiatt 1948). Fertilized eggs are extruded, attached to the females pleopods on the abdomen, and brooded for 26 to 31 days prior to hatching (Hiatt 1948). Following hatching, larval development of *P. crassipes* is thought to include 6 zoeal stages (Jose Cuesta, pers. comm.) followed by a post-larval megalopal stage. Schlotterbeck (1976) reported a mean duration of 115 d for zoea reared to the fifth stage of development under laboratory conditions.

This study examined the effects of brood site (site of origin) and culture water source on the survival and rate of development of *P. crassipes* larvae. Newly released larvae originating from three sites were reared in the laboratory in waters from each site through to the megalopal stage. The null hypothesis was that there are no differences in the development rate or survival of zoeae brooded in or developing in waters of southern Californian embayments when compared with zoeae developing in a nearby exposed coastal environment.

Methods

Culturing experiments

A laboratory experiment was conducted to examine the effects of site of larval origin and culture water on larval mortality and development. Ovigerous crabs, *Pachygrapsus crassipes,* were collected from three sites in southern California, USA, including two embayments (1) Sweetwater Marsh, San Diego Bay (SDB)(Chula Vista, California), and (2) the Northern Wildlife Preserve, Mission Bay (MB) (Pacific Beach, California), and one open coastal site (3) Dike Rock (DR), La Jolla Shores Beach (La Jolla, California) (Fig. 1). Sweetwater Marsh is located in the inner half of SDB, 17 km from the bay's entrance. The Northern Wildlife Preserve is located in the northeast corner of MB, 5 km from the bay entrance. Dike Rock is a coastal rocky intertidal habitat, located on the open coast, 24 km north of the entrance to SDB. Ovigerous females were collected between 29 June and 29 July 1996 (Table 1) and transported back to the lab in plastic coolers containing local, ambient temperature seawater within 1-2 hours of collection. Females were transferred to a temperature controlled culture room (20 °C-22 °C) and held in a 14 h light/10 h dark schedule simulating *in situ* conditions. Each ovigerous female was placed into an acid-washed, high-density polyethylene (HDPE) bowl filled with 4 L of 5-μm filtered seawater collected at the same sites

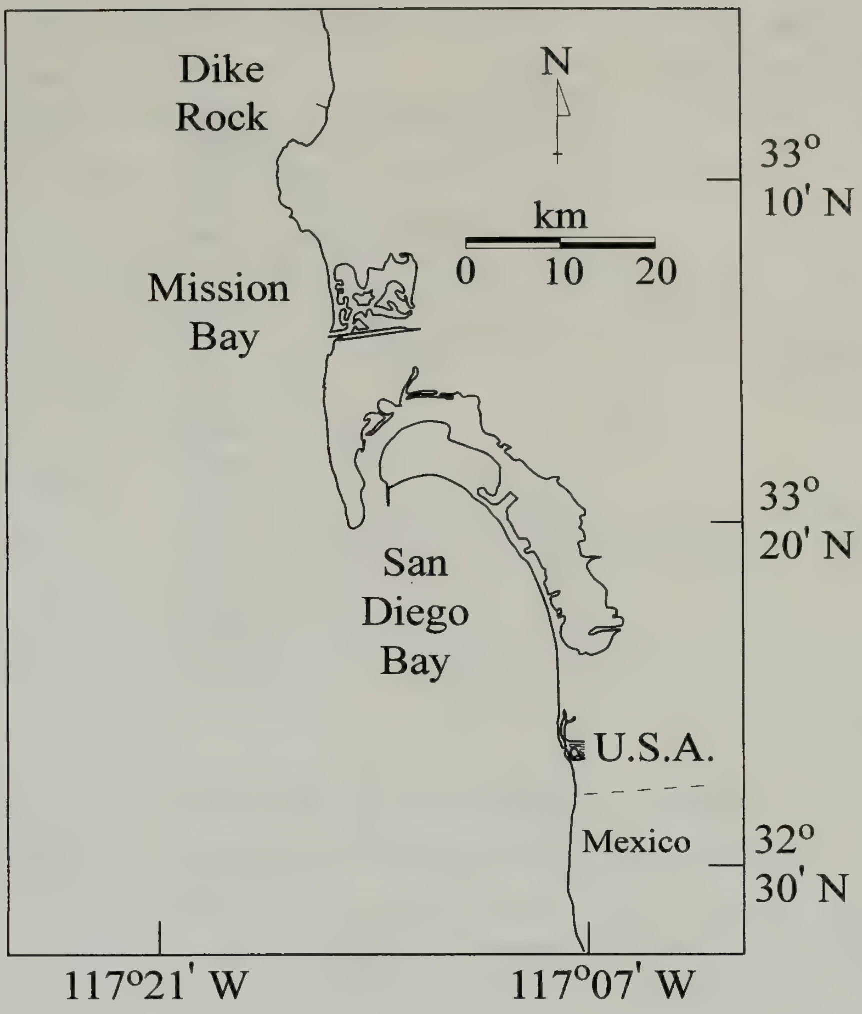

Fig. 1. Location of three collection sites for ovigerous shore crabs, *Pachygrapsus crassipes,* and culture water in southern California. Sites include two embayments, Sweetwater Marsh, San Diego Bay and the Northern Wildlife Preserve, Mission Bay, and one open coastal site, Dike Rock, La Jolla Shores Beach.

and times as crabs (SDB, 34.3 ± 1.4 psu (practical salinity units, average ± SD); MB, 32.2 ± 1.5 psu; DR, 32.8 ± 1.4 psu). All containers were aerated using standard aquarium air pumps and were covered to avoid evaporation and changes in salinity. Laboratory culture water was collected by pumping subsurface (> 0.5 m) seawater through a filter bag and into prewashed (10% Nitric Acid, rinsed in 18 mΩ water), 20-L HDPE carboys for transport back to the lab. Once in the laboratory, all water was passed through a 5-μm filter. Filtered seawater was maintained in the dark at a temperature of 18 °C and replaced every week. Ovigerous females were not fed. Zoeae hatching within 36 h of the female collection date were used to provide larvae for culturing experiments (Table 1).

A total of 12 females, 4 from each of three sites, were used in this study (Table 1). Zoeae hatched from individual females were sub-sampled into 3 groups of 200 individuals. The three groups were reared in source water collected from SDB, MB or DR, respectively. Larvae in each treatment were reared under static conditions in 4 L of seawater in HDPE bowls at 200 individuals per bowl (50 zoeae L^{-1}) on a diet of newly hatched brine shrimp nauplii (*Artemia* sp.) at a density of 4000 nauplii L^{-1}. All larvae were fed freshly hatched brine shrimp (*Artemia* sp.) nauplii that had been reared in seawater corresponding to the respective culture water treatment. In addition to maintaining culture water temperature (20 °C-22 °C) and salinity (33.28 ± 1.13 psu; mean ± SD) at ambient conditions, oxygen concentration and pH were monitored to ensure that they were

Table 1. Collection site, date collected and date hatched for ovigerous crabs, *Pachygrapsus crassipes,* employed in larval culturing experiments.

Collection site	Individual	Date collected	Date hatched
Sweetwater Marsh, San Diego Bay, CA	1	29 June 1996	30 June 1996
	2	1 July 1996	2 July 1996
	3	29 July 1996	30 July 1996
	4	29 July 1996	30 July 1996
Northern Wildlife Preserve, Mission Bay, CA	5	1 July 1996	2 July 1996
	6	1 July 1996	3 July 1996
	7	15 July 1996	16 July 1996
	8	15 July 1996	16 July 1996
Dike Rock, La Jolla Shores Beach, La Jolla, CA	9	1 July 1996	3 July 1996
	10	13 July 1996	14 July 1996
	11	13 July 1996	15 July 1996
	12	29 July 1996	30 July 1996

maintained close to ambient conditions, thus minimizing their effect on zoeal survivorship and development. Larvae were transferred to clean culture bowls with fresh seawater every 48 h; food rations were replenished daily.

Larval cultures were monitored every second day. Dead individuals were tallied and removed while live zoeae were transferred to fresh seawater. Larvae were examined under a dissecting microscope and considered dead when no body movements or a beating heart were visible. Cultures were maintained until all larvae had either died or metamorphosed into post-larval megalopae. Magalopae were held individually in containers identical to those used to culture zoeae. They were supplied with fresh seawater every second day and fed newly hatched brine shrimp nauplii and commercial brine shrimp flakes daily.

Statistical analysis

The following parameters were evaluated: (i) zoeal survivorship, (ii) zoeal duration (number of days from hatching to stage VI for surviving larvae) expressed as average time to megalopa (ATM *sensu* Epifanio *et al.* 1998), (iii) percentage of stage I zoeae surviving to the megalopal stage of development, (iv) percentage of zoeae that molted from stage VI zoea to the megalopal stage, and survival time of megalopae reared in this experiment. One-way and two-way analysis of variance (ANOVA) models were used to evaluate site of larval origin (SDB, MB, DR) and source water (SDB, MB, DR) effects on larval survivorship and rates of development. A repeated measures analysis, using a two-way ANOVA model, was used to test site of origin and source water effects on zoeal survivorship independent of time. Two-way ANOVA models were used to assess brood site and culture water effects only when no significant interactions were observed. If an interaction term was significant, each factor was analyzed independently using a 1-way ANOVA model. All post-hoc multiple comparisons were conducted with the Student-*t* statistic, using a Bonferroni correction (Type I error) where multiple comparisons were made. Percent data were arcsine transformed prior to analysis.

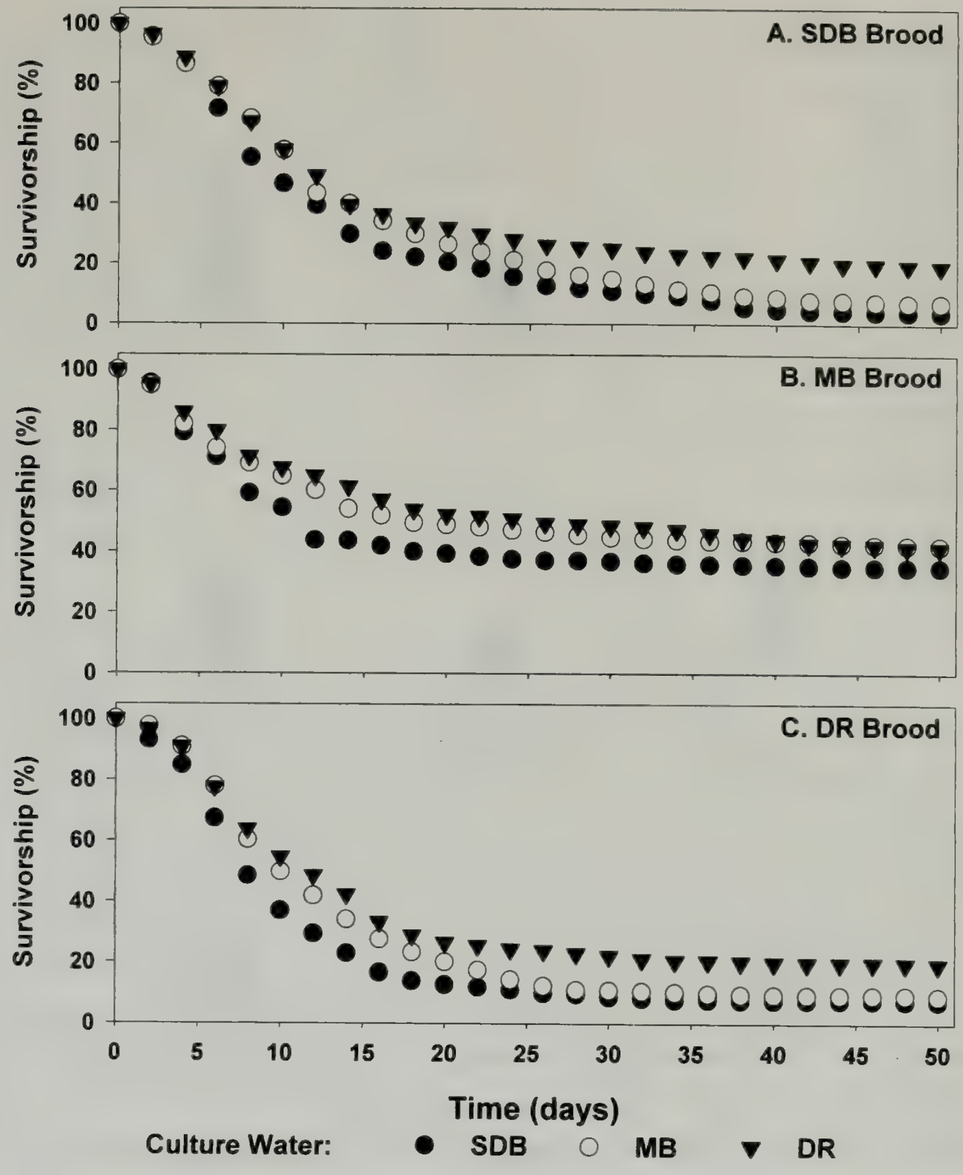

Fig. 2. Culture water effects on laboratory cultured crab larvae, *Pachygrapsus crassipes,* expressed as percent survivorship. Mean survivorship estimates within each plot (A-C) are independent of larval origin since larvae were brooded in (A) Sweetwater Marsh, San Diego Bay (SDB), CA, (B) Northern Wildlife Preserve, Mission Bay (MB), CA, or (C) Dike Rock (DR), La Jolla, CA. All curves are terminated at day 50, but cultures lasted an average of 98 ± 7 d (SD). Error bars are not shown for the sake of clarity. Statistical comparisons among sites are given in the text.

Results

Zoeal Survivorship

Zoeae in culture survived an average of 98 ± 7 d (mean ± SD). Larval brood site (Repeated Measures Analysis, 2-way ANOVA model; $F_{2,26} = 11.261$, $p<0.001$) and culture water ($F_{2,26}=3.745$, $p=0.037$) both had a significant effect on zoeal survivorship. The interaction term was not significant ($F_{4,26}=0.121$, $p=0.974$). Zoea cultured in DR seawater had 14% higher survivorship than those reared in SDB seawater (Student-*t*; $t_{0.05(2),21}=2.080$, $p=0.0211$)(Fig. 2). Zoeae reared in MB seawater did not differ significantly from zoeae reared in either DR (Student-*t*; $t_{0.05(2),22}=2.074$, $p=0.247$) or SDB seawater (Student-*t*; $t_{0.05(2),21}=2.080$, $p=0.229$). Zoeae brooded in MB experienced 21% and 24% higher survivorship than those brooded in either SDB (Student-*t*; $t_{0.05(2),21}=2.080$, $p=0.004$) or the DR habitat, respectively (Student-*t*; $t_{0.05(2),21}=2.080$, $p<0.001$). Zoeae brooded in SDB and the DR habitat exhibited similar survivorship (Student-*t*; $t_{0.05(2),22}=2.074$, $p=0.420$).

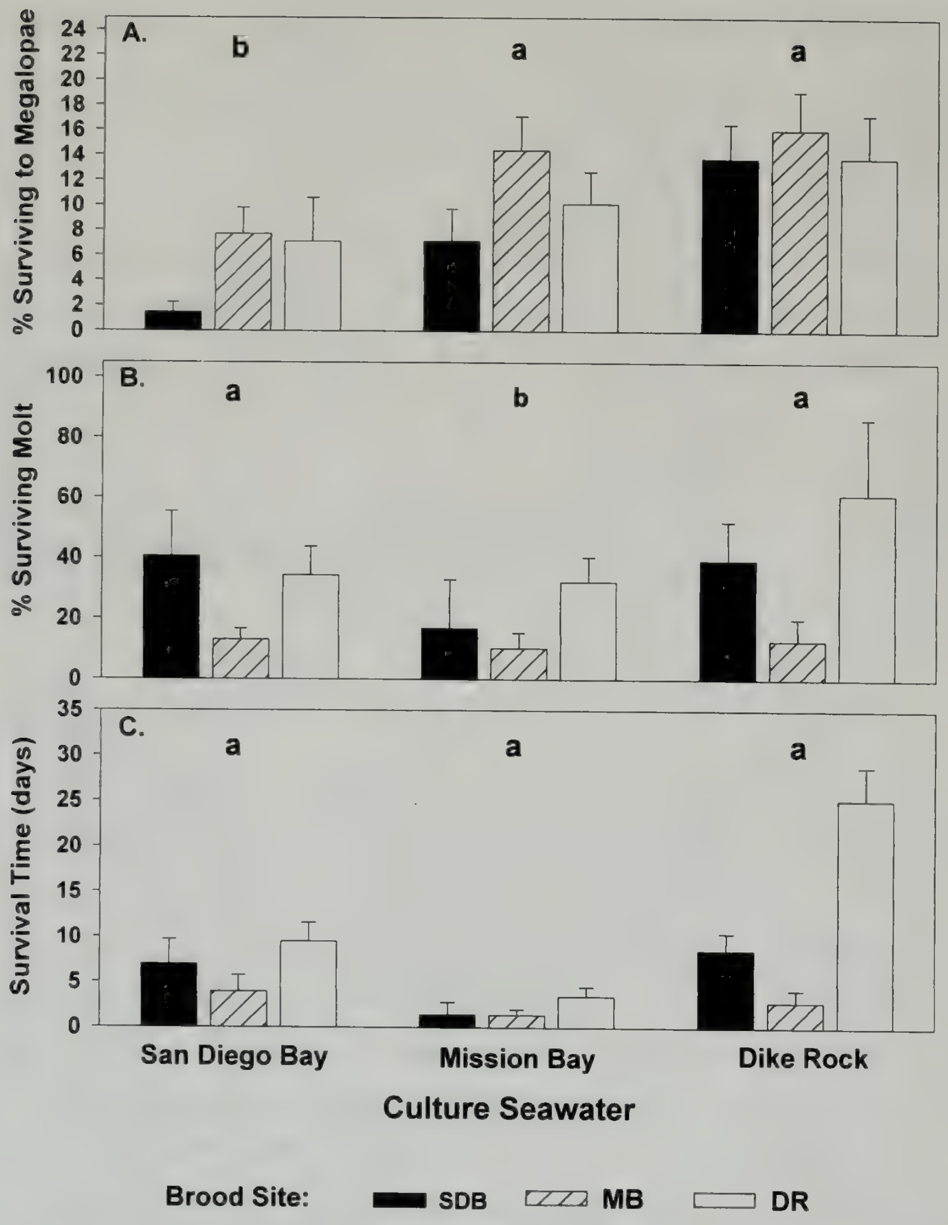

Fig. 3. Culture water and brood site effects on (A) the mean percentage of stage I zoeae, *Pachygrapsus crassipes,* surviving to the megalopal stage of development, (B) the mean percentage of stage VI zoeae, *Pachygrapsus crassipes,* which molted from the sixth zoeal stage to the megalopal stage, and (C) the survival time (days) for laboratory cultured crab megalopae, *Pachygrapsus crassipes* since molting from the sixth zoeal stage of development. Error bars indicate ±1 SE. MB= Mission Bay, SDB= San Diego Bay, DR= Dike Rock. Culture water treatments sharing the same letter (a, b) are not significantly different. Brood site results are given in the text.

Development Time

Laboratory-based estimates of ATM (mean zoeal duration, stages I through VI) for individual *P. crassipes* larvae ranged from 68 d to 108 d. There were no significant differences in ATM for *P. crassipes* zoeae as a function of brood site (2-way ANOVA, $F_{2,19}=0.287$, $p=0.754$) or culture water ($F_{2,19}=0.021$, $p=0.979$; interaction term, $F_{4,19}=0.294$, $p=0.878$).

Survival to Megalopae

Source water had a significant effect on the percentage of zoeae surviving to the megalopal stage of development (2-way ANOVA, $F_{2,18}=8.578$, $p=0.002$), while differences due to the site of larval origin were not significant ($F_{2,18}=3.306$, $p=0.060$; interaction term, $F_{4,18}=0.681$, $p=0.614$) (Fig. 3A). Cultures reared in SDB seawater yielded a significantly lower percentage of megalopae (3.6 ± 1.9%; mean ± SD) than those reared in DR seawater (14.5 ± 5.5%; Student-*t*;

$t_{0.05(2),16}=2.120$, $p=0.002$) or MB water (10.5 ± 5.5%; Student-*t*; $t_{0.05(2),16}=2.120$, $p=0.040$). The percentage of megalopae produced from zoeae cultured in DR or MB seawater did not differ statistically (Student-*t*; $t_{0.05(2),16}=2.120$, $p=0.125$).

The percentage of stage VI zoeae that successfully molted to the megalopal stage of development ranged from 10.2% to 61.1% across brood site and culture water treatments (Fig. 3B). Culture water had a significant effect on the survival of stage VI zoeae molting to the megalopal stage of development (2-way ANOVA, $F_{1,8} = 5.400$, $p=0.013$) while brood site did not ($F_{1,8}=2.162$, $p=0.141$; interaction term, $F_{1,8}=0.923$, $p=0.470$). Stage VI zoeae reared in MB seawater experienced significantly lower molting success (11.3 ± 8.5%; mean ± SD) than those reared in DR (37.9 ± 22.0%; Student-*t*; $t_{0.05(2),17}=2.110$, $p=0.005$) or SDB seawater (30.7 ± 24.0%; Student-*t*; $t_{0.05(2),17}=2.110$, $p=0.030$).

Megalopal Duration

The majority of larvae reaching the larval megalopal stage (474 of 481 individuals) did not metamorphose (i.e., settle) to the juvenile stage of development. *Pachygrapsus crassipes* megalopae settle and then metamorphose in intertidal or high intertidal habitats (e.g., mussel beds, seagrass) (Hiatt 1948; DiBacco, unpublished data). The lack of any settlement substrate in culture containers employed in this study may have inhibited metamorphosis to the juvenile stage. The length of time that megalopae survived (Survival Time, Fig. 3C) is interpreted here as a measure of their overall fitness in culturing conditions. Megalopae that successfully metamorphosed to the juvenile stage are not considered here since they represent only 5.1% (n=26 ind.) of total megalopal observations. A 2-way ANOVA on survival time revealed an interaction between culture water and brood site ($F_{1,8}=2.661$, $p=0.142$); therefore these factors were analyzed separately with 1-way ANOVA. Site of larval origin (1-way ANOVA, $F_{2,22}=11.089$, $p<0.001$) had a significant effect on survival time, but source water did not ($F_{2,22}=2.017$, $p=0.157$). Megalopae originating from MB survived significantly less time (2.3 ± 7.6 d) than those originating from the DR site (10.0 ± 17.4 d, Student-*t*; $t_{0.05(2),14}=2.145$, $p=0.002$) or from SDB (7.2 ± 14.3 d; Student-*t*; $t_{0.05(2),14}=2.145$, $p=0.004$). Megalopal survival time in SDB and the DR site did not differ (Student-*t*; $t_{0.05(2),16}=2.120$, $p=0.636$).

Discussion

Our results suggest that *P. crassipes* zoeae cultured or brooded in bay seawater (SDB or MB) experienced lower survivorship and produced fewer megalopae than zoeae brooded or reared in coastal (DR) seawater, with the exception of MB brooded zoeae which had higher survivorship than larvae brooded in either SDB or DR. These results have implications for the source of individuals recruiting to adult populations. If larvae originating from SDB are less likely to survive and ultimately settle than those from other bays, other sites may be responsible for maintenance of SDB populations. Reduced survivorship of larvae in SDB habitats with no change in development time would favor recruitment by larvae that were brooded and which develop in coastal waters. Organisms which either inhabit both bay and coastal habitats, or whose larvae can be found in both environments during all stages of development, may experience preferential recruitment than larvae brooded and/or developing in coastal water. If bay populations are selfseeding, reduced availability of recruits could result in reduced population size and ultimately local extinction.

Residence time estimates for SDB seawater, in the region of the Sweetwater Marsh, are on the order of 100 days (Chadwick *et al.* 1996, Chadwick & Largier 1999). Planktonic larvae that disperse passively would spend most or all of their time in the bay. *Pachygrapsus crassipes* zoeae sampled in SDB during consecutive ebbing and flooding tides exhibited tidally timed, vertical migratory behavior (DiBacco 1999). They concentrate in surface waters during nighttime ebbing tides and on or near the sediment surface (<1 meter above bottom [mab], including the sediment-water interface) during flood conditions (DiBacco 1998). This migratory behavior, which has been observed for other grapsid crabs (Christy and Stancyk 1982), should promote transport out of SDB and drastically reduce the residence time of zoeae within the bay. Larvae leaving SDB for open coastal waters should experience increased probability of surviving to the megalopal stage (Fig. 3A).

The survivorship estimates reported in this study are comparable to those of grapsid crab larvae in other studies. Survivorship through the last stage of zoeal development of *P. crassipes* in the present study ranged from 3 % to 15 % at relatively constant temperatures (20 °C-22 °C) and salinities (31 %-32 %) selected to mimic ambient conditions. Schlotterbeck (1976) reported 0 % survivorship for *P. crassipes* with no zoeae surviving through the fifth zoeal stage (V) of development reared under similar temperature, salinity and food conditions in the laboratory. Other laboratory studies have reported survivorship estimates between 0 % and 60 % for grapsid crab larvae reared under comparable temperature and salinity conditions (*Armases cinereum,* formerly *Sesarma cinereum,* see Costlow *et al.* 1960; *Hemigrapsus sanguineus,* see Epifanio *et al.* 1998). The ATM for *P. crassipes* zoeae (from hatching to the megalopal stage of development) observed in this study (84 d from stage I to megalopa) was shorter than estimates reported by Schlotterbeck (1976) for the same species (86 d from stage I to stage IV). The duration of zoeal development reported for zoeae of other grapsid crab species can be considerably shorter; e.g., 15 to 55 d for *Hemigrapsus sanguineus* (Epifanio *et al.* 1998) and 20 to 28 d for *Armases cinereum* (Costlow *et al.* 1960). The longer duration of *P. crassipes* zoeal development seems to reflect a characteristic difference in development rate among the species mentioned above. Since *P. crassipes* zoeal development time is much greater than that of other grapsid crabs, survivorship differences due to brood site or culture water may be especially important in determining the source of successful recruits to adult populations.

Site of larval origin (i.e., brood site) as well as subsequent dispersal and transport are important in determining exposure times to potentially toxic environments. One factor not controlled in this study was anthropogenic pollutants. Significantly higher mean trace element concentrations were found in stage I zoea originating from SDB ($Cu=25.3\ \mu g \cdot kg^{-1}$, $Al=34.1\ \mu g \cdot kg^{-1}$, $Zn=25.8\ \mu g \cdot kg^{-1}$) when compared with larvae collected from coastal habitats ($Cu=1.0\ \mu g \cdot kg^{-1}$, $Al=8.9\ \mu g \cdot kg^{-1}$, $Zn=3.4\ \mu g \cdot kg^{-1}$)(DiBacco & Levin, in press). Elevated body burden estimates and seawater composition suggest that trace elements could contribute to reduced survivorship observed in SDB brooded and cultured larvae. Trace elemental toxicants are sources of physiological stress and can account for reduced survivorship and development in marine invertebrate larvae (Kennish 1992). San Diego Bay, which has been heavily impacted by industrial, commercial and military development, has been ranked as one of the most contaminated urbanized coastal areas in the nation (O'Connor 1990). San Diego Bay pollutants include nutrient enrichment via organic wastes (sewage, fertilizers), hydrocarbons (PAHs), chlorinated hydrocarons (PCBs, pesticides), and heavy metals (copper, aluminum, zinc). These contaminants are introduced to the marine coastal environments directly through industrial, commercial, and military activities or by way of rainwater runoff (non-point source) from thousands of acres of urban development in the SDB watershed (McCain *et al.* 1992; Flegal & Sañudo-Wilhelmy 1993; SWRCB & NOAA 1996; Kennish 1998). Although elevated concentrations of toxicants in SDB are likely to have an effect on the survivorship and development of *P. crassipes* larvae, the experimental design employed here does not allow us to isolate effects due to elemental toxicants and other sources of pollution.

The exposure of larvae to pollutants *in situ* may fluctuate as a result of intermittent additions of polluting substances or due to the dispersal and transport of larvae between regions of an embayment or between bay and coastal environments. The ability of *P. crassipes* to migrate vertically and enhance transport out of SDB to more pristine coastal environments could reduce harmful developmental effects associated with SDB water. Ringwood (1992) showed that larvae of a bivalve, *Isognomon californicum,* exposed to ambient concentrations of selected trace elements initially suffered severe adverse effects. However, these effects were reversible if the toxicant was removed from the larva's environment prior to permanent damage. Ringwood's (1992) results and those presented here for *P. crassipes* suggest that both larval source and larval trajectories in bay and coastal settings can have a major influence on the dynamics of the larval phase, and potentially on the structure of populations. Methods that reveal larval site of origin or transport pathways and rates will contribute significantly to understanding the dynamics of estuarine and coastal species.

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Research Report

New Geographical Records of Nine Species of Crustaceans from Southern Baja California, Mexico

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Surveys on Baja California coasts allow us to report new geographical records of 9 species of crustaceans (1 stomatopod, 5 caridean shrimps and 3 brachyuran crabs). The new records update those of Wicksten & Hendrickx (1992), Hendrickx (1995) and Hendrickx & Landa-Jaime (1997). The following abbreviations are used: total length, TL; carapace width, CW; carapace length, CL.

Order Stomatopoda
Family Squillidae
Squilla tiburonensis Schmitt 1940

Previous distribution.—From Consag Rock to Espiritu Santo and Punta Piaxtla Gulf of California, Mexico (Hendrickx & Salgado-Barragán 1991).

New records.—3 males (TL 77–87 mm) and 6 females (TL 60–84 mm), taken on December 21, 1997 during shrimp trawling operations, depth 58.7 m, Asuncion Bay, 27°06′45″ N, 114°15′43″ W, west coast of Baja California, Mexico.

Order Decapoda
Family Alpheidae
Synalpheus biunguiculatus (Stimpson 1860)

Previous distribution.—Guaymas, Gulf of California, Mexico to Colombia; Clarion, Clipperton and Malpelo Islands; Hawaii (Wicksten & Hendrickx 1992).

New records.—1 ovigerous female (TL 24.8 mm), March 3, 1998, collected in lobster larvae traps, depth 6 m, Punta Abreojos, 26°45′40″ N, 113°30′58″ W, west coast of Baja California, Mexico.

Family Hippolytidae
Hippolyte williamsi Schmitt 1924

Previous distribution.—Puerto Peñasco, Gulf of California, Mexico to Mejillones Bay, Chile; Galapagos Islands (Wicksten & Hendrickx 1992).

New records.—4 males (TL 14.7–18.9 mm), 5 females (TL 13.2–18.6 mm) and 12 ovigerous females (TL 15.8–19.4 mm), March 3, 1998, collected in lobster larvae traps, depth 6 m, Punta Abreojos, 26°45′40″ N, 113°30′58″ W, west coast of Baja California, Mexico.

Thor cordelli Wicksten 1996

Previous distribution.—Rocas Alijos and Clarion Island, Mexico; Punta Alta, Colombia (Wicksten 1996).

New records.—1 ovigerous female, (TL 14.1 mm), March 3, 1998, collected in lobster larvae traps, depth 6 m, Punta Abreojos, 26°45′40″ N, 113°30′58″ W, west coast of Baja California, Mexico.

Family Palaemonidae

Neopontonides dentiger Holthuis 1952

Previous distribution.—Baluarte River, Sinaloa, Mexico to Cabo San Francisco, Ecuador (Wicksten & Hendrickx 1992).

New records.—1 male (TL 24.6 mm) and 2 ovigerous females (TL 27.2–27.7 mm), March 3, 1998, collected in lobster larvae traps, depth 6 m, Punta Abreojos, 26°45′40″ N, 113°30′58″ W, west coast of Baja California, Mexico.

Palaemonetes hiltoni Schmitt, 1921

Previous distribution.—San Pedro, U.S.A; Guaymas and Caimanero Lagoon, Gulf of California, Mexico (Wicksten & Hendrickx 1992).

New records.—7 males (TL 22–32.5 mm), 12 females (TL 22–30.7 mm) and 3 ovigerous females (TL 33.7–34.9 mm), March 3, 1998, collected in lobster larvae traps, depth 6 m, Punta Abreojos, 26°45′40″ N, 113°30′58″ W, west coast of Baja California, Mexico.

Remarks.—Wicksten (1989) remarked that this species "has not been reported from Southern California since its description in 1921." *Palaemonetes hiltoni* is rare on the Pacific coast of Baja California, existing predominantly in the Gulf of California: Sonora and Sinaloa, Mexico (Holthuis 1952).

Family Epialtidae

Acanthonyx petiveri H. Milne Edwards 1834

Previous distribution.—From Santa Maria Bay, west coast of Baja California, La Paz and Mazatlan, Gulf of California, Mexico to Valparaiso, Chile; Revillagigedo and Galapagos Islands; Western Atlantic (Hendrickx 1995).

New records.—2 males (CW 9.8–10.5 mm, CL 12.8–14 mm) on February 28, 1998, intertidal under rocks at Punta Abreojos, 26°42′30″ N, 113°34′30″ W, west coast of Baja California, Mexico.

Epialtus minimus Lockington 1877

Previous distribution.—From 28°12′N, west coast of Baja California, and throughout the Gulf of California to Acapulco, Mexico (Hendrickx 1995).

New records.—1 male (CW 9.5 mm, CL 10.5 mm) on February 28, 1998, intertidal, under rocks at Punta Abreojos, 26°42′30″ N, 113°34′30″ W, west coast of Baja California, Mexico.

Remarks.—The presence of this species outside the Gulf of California was considered an extralimital record (Garth 1958). Therefore, the record provided herein confirms the presence of *Epialtus minimus* on the west coast of Baja California.

Family Parthenopidae
Parthenope johngarthi Hendrickx & Landa-Jaime 1997

Previous distribution.—From Tenacatita Bay, Jalisco to Manzanillo, Colima, Mexico (Hendrickx & Landa-Jaime 1997).

New records.—1 male (CW 43 mm, CL 34 mm) and 1 female (CW 39 mm, CL 29 mm) taken on May 23, 1999 collected by J. Fiol with baited traps, depth 75 m, at La Ventana, 24°05′59″ N, 109°57′08″ W, La Paz, Gulf of California, Mexico.

Remarks.—This species has been recently described, the northern-most record of which was from Tenacatita Bay, Jalisco, Mexico. This is the first report in the Gulf of California and constitutes the northern-most record.

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Potential Impacts of *Pogonomyrmex rugosus* on *Larrea tridentata* in southern California

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The seed harvester ant (*Pogonomyrmex rugosus*) occurs in arid and semiarid plant communities throughout much of the southwestern United States (Carlson and Whitford 1991). *Pogonomyrmex rugosus* discs (nests) are often surrounded by conspicuous clearings from which the ants have actively removed the vegetation. *Pogonomyrmex rugosus* colonies are located preferentially near creosote bush (*Larrea tridentata*), and *P. rugosus* may cause mortality of *L. tridentata* by defoliation in southern Nevada (Rissing 1988). Shrubs may initially provide valuable shade to establishing ant colonies; yet, later in colony ontogeny, shrubs compete with ants for water in southern Nevada (Rissing 1988). From casual observations, size of and proximity to a *P. rugosus* colony appear to influence viability of *L. tridentata* in southern California.

The xerophytic *L. tridentata-Ambrosia* dumosa (white bursage) shrubland is a common vegetation type in the Mojave Desert of southern California. In a 5-ha site, viability of *L. tridentata* appears to be greatly reduced by the presence of numerous ant colonies. The objectives of this study are two-fold: 1) Are the *P. rugosus* nests in the 5-ha site located closer to the nearest *L. tridentata* than expected based upon an assumption of random distribution? 2) Are more *L. tridentata* plants found to be dead in proximity to ant nests?

The study site, predominated by evergreen *L. tridentata* shrubs, was near Baker, California (roughly 35′05°N, 115′55°W; elevation 715 m). Other woody species are sparsely distributed in this vegetation zone, including white bursage (*A. dumosa*), ratany, (*Krameria parvifolia*), Mojave yucca (*Yucca schidigera*), goldenhead (*Acamptopappus shockleyi*), indigo bush (*Psorothamnus fremontii*), and brittle bush (*Encelia virginensis*). Soils are sandy in texture, and are calcareous with abundant loose rocks on the surface. Soils are derived from limestone-dolomite mountains and hills (Rowlands et al. 1977).

The spatial distribution of *P. rugosus* nests and the nearest *L. tridentata* shrubs was examined at a 5-ha site. All 206 ant nests in the site were identified. Each ant colony had multiple nest entrances, with a construction of subterranean chambers (cavities) and runways. Diameters of the exposed soil surface (disc) at each ant colony were measured in centimeters by computing the average of length and width of the nest. A farthest point was established at a 4-m radius from the center of each ant nest. Condition of the *L. tridentata* shrub closest to the center of each *P. rugosus* colony was recorded as either live or dead. Shrubs with green leaves on secondary branches were considered alive. The distance (cm) from the center of the ant colony to the center of the nearest *L. tridentata* was measured. The numbers of live and dead shrubs within the 4-m radius zones (plots) centered on

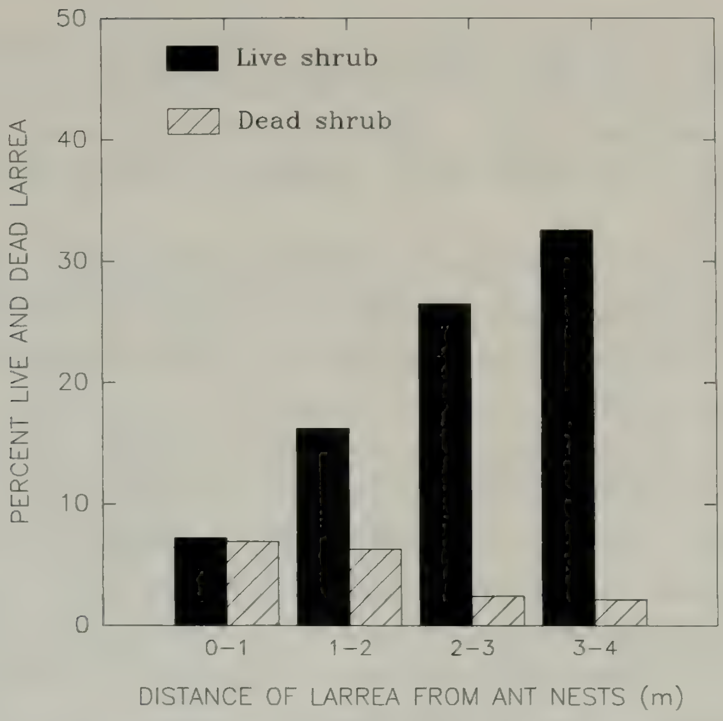

Fig. 1. Condition of *L. tridentata* (live and dead) in plots of 4-m radius centered on *P. rugosus* colonies near Baker, California.

ant nests were recorded and were converted into percentages. These zones were subdivided into four, 1-m radius increments.

Mean distance between the centers of ant colonies and nearest shrub was obtained for observations. The ratio of the observed mean distance to the expected mean distance (R-value) served as a measure of departure from randomness (Clark and Evans 1954). The nearest neighbor method (Clark and Evans 1954) was used to determine whether the *P. rugosus* colonies were randomly distributed in the habitat with respect to *L. tridentata.* The significant difference in the value of R for these two populations was tested at the 0.05 level by the Student-Fisher t distribution (McClave and Dietrich 1991).

Pogonomyrmex rugosus colonies and the nearest *L. tridentata* shrubs were strongly aggregated, with an R value of 0.23. The mean distance between the centers of ant colonies and nearest shrubs was 179.7 ± 10.5 cm. The mean diameter of ant colonies (disc) was 81.8 ± 8.2 cm ($n = 206$).

The greatest percentage of live *L. tridentata* shrubs was found between 3 to 4-m radius plots from the center of *P. rugosus* nests (Fig. 1). Conversely, the percentage of dead shrubs, with no green leaves on secondary branches, was highest within the 1-m radius plots centered on ant nests. Percentages of live and dead shrub were nearly equal within the 1-m radius plot (Fig. 1). The centers of ant nests were generally clear of *L. tridentata* plants. Although many shrubs were considered alive, a substantial leaf defoliation by ants was evident, especially *L. tridentata* establishing within the 2-m radius plots from the center of ant nests.

Pogonomyrmex rugosus colonies and the nearest *L. tridentata* shrubs exhibited strong aggregation. For the spatial distribution in this study, $R = 0.23$, indicating a significant departure from random expectation in the direction of aggregated spacing by the c test. According to the distance to nearest neighbor as a measure of spatial distribution in populations, $R = 0$ in a maximum aggregation, since all of the individuals occupy the same locus and the distance to nearest neighbor is therefore 0. In contrast, $R = 2.1491$ in a maximum uniformity, since individuals will be distributed as evenly and widely as possible in a hexagonal pattern (Clark and Evans 1954). The ratio of observed to expected mean distance to nearest neighbor provides a measure of the degree to which the distributional pattern of the observed population deviates from random expectation (Clark and Evans 1954).

Subterranean *Pogonomyrmex rugosus* are located preferentially near *L. tridentata* shrubs in some microhabitats at a Mojave Desert site (Rissing 1988), which is in agreement with this study. *Pogonomyrmex rugosus* may select nesting sites in consideration of proximity to nearby shrubs. In this study, a higher mortality rate was observed for *L. tridentata* shrubs near ant nests than those distributed randomly. The interaction is potentially detrimental for shrubs; shrubs nearest ant nests have significantly reduced viability, and defoliation of leaves by ants may cause mortality of shrubs in southern Nevada (Rissing 1988). Rissing (1988) saw *P. rugosus* defoliating leaves of surrounding *L. tridentata. Pogonomyrmex rugosus* probably are attempting to reduce nest shading by removing leaves through time. Most ant colonies in the genus *Pogonomyrmex* require high temperatures for brood development (Clark and Comanor 1975).

The "disc" is a visually obvious nest structure, but the limits of the nest itself may extend below the soil surface at a distance beyond the "disc" (Lei 1999). The subterranean *P. rugosus* colony also has influences on the soil surface beyond the limits or physical structure of the nest disc (Lei 1999).

Although the total area covered by active *P. rugosus* nests was relatively small, subterranean *P. rugosus* greatly reduced the viability of *L. tridentata* beyond the nest discs. *Pogonomyrmex rugosus* preferentially established nests near *L. tridentata.* A substantial *L. tridentata* mortality within the 2-m radius plots centered on ant nests was observed, primarily due to multiple nest entrances with extremely high social activities. Despite a considerable leaf defoliation by ants, *L. tridentata* plants had the greatest percentage of green leaves on their branches when establishing away from the nest discs near Baker, California.

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The BULLETIN is published three times each year (April, August, and December) and includes articles in English in any field of science with **an emphasis on the southern California area**. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

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